Recruitment of a Long-term-memory Supporting System During Repeated Maintenance of an Abstract Visual Image in Working Memory: An EEG Study

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Research Article

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Posted Date: June 7th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-569099/v1>

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**Recruitment of a long-term-memory supporting system during repeated maintenance of
an abstract visual image in working memory: an EEG study.**

Short: Long term memory system in visual working memory.

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Abstract

Humans can flexibly transfer information between different memory systems. Information in visual working memory (VWM) can for instance be stored in long-term memory (LTM) when a scene is repeatedly memorized. Conversely, information can be retrieved from LTM and temporarily held in WM when needed. It has previously been suggested that a neural transition from parietal- to midfrontal activity reflects transfer of information from WM to LTM during repeated visual search for the same single item. However, whether these observed neural changes truly represent consolidation and are also observed when memorizing and (explicitly) recollecting a rich visual scene (rather than a single target), remains unclear. The current EEG study investigates whether such a gradual shift in memory-correlates is also observed when an abstract colour-array is repeatedly memorized and explicitly recollected in a WM paradigm. Importantly, we tested the functional significance of a neural shift for longer-term consolidation in a subsequent recognition task.

Our results provide supporting evidence for recruitment of an LTM-supporting storage system during WM, which facilitates visual WM maintenance and is indexed by (sustained) modulation of a midfrontal component. Enhanced explicit memory recollection during WM is associated with- and possibly facilitated by an emerging late contralateral parietal activity.

Keywords: Attention, Working Memory, Long-Term Memory, Explicit Recollection, EEG, Contra-lateral Delay Activity, Midfrontal Activity.

1. Introduction

When an artist paints a landscape from life, at first the chosen scene will need to be inspected regularly, but gradually a detailed picture may develop in the painter's mind. How is the image represented in the brain and how does this representation change, when the artist becomes more familiar with the depicted landscape? The current EEG study investigated whether a shift in mnemonic representation can be observed during learning of an abstract visual scene. Based on an earlier study, which reported a transition in memory-sustaining neural representations when subjects became gradually more efficient in spotting a visual search target¹⁻³, we specifically looked at parietal- and midfrontal components.

The ability to hold representations of several visual items online for direct access and manipulation by higher cognitive functions, is known as visual working memory (WM). There is a capacity limit to the number of items that can be contained in visual WM, which usually sits around 4, but differs across individuals⁴. While traditionally visual WM is thought to rely on a frontal-parietal network, recent evidence suggests that it can recruit MTL/hippocampal structures as well, perhaps particularly when the number of memorized items exceeds the visual WM capacity limit and/or when spatial location is an important dimension of the memory trace (see⁵ for a review). A proven EEG method to measure several aspects of visual WM, such as capacity and filtering efficiency, is the contralateral delay activity (CDA). This is a sustained negativity around parietal-occipital electrodes which scales with the number of memorized items^{4,6} (and see⁷ for a review) and can also be observed while a search template is held online during visual search⁸.

In the previously mentioned study¹, it was shown that the CDA amplitude gradually decreases in amplitude during repeated and increasingly efficient search for the same target in different search contexts². The decrease in CDA amplitude concurred with a negative modulation of a

midfrontal P170 component, which was interpreted as a transfer of information between a WM- to a long-term memory (LTM) store. Whether this shift in neural correlates is really linked to an enhanced consolidation of the visual memory trace can however not be concluded from this study, as recognition was not tested afterwards. In addition, a more efficient search performance is likely to reflect (perhaps implicit) short-term strengthening of stimulus-response connections (see ⁹), but not necessarily an enhanced *explicit* memory representation.

Negative modulation of the midfrontal P170 component has indeed been associated with long-term (implicit) memory processes such as perceptual priming¹⁰, involving perceptual categorization and grouping processes^{11,12}. Many other studies have implicated a later (positive) midfrontal component in conscious recognition ^{13,14}. In these studies, a dissociation emerges between recognition based on familiarity (knowing), signaled by the midfrontal component, versus rich detailed recollection, reflected in a later parietal activity³⁰⁻³⁸.

The scalp location of the midfrontal signal (around the Fz electrode) may link this activity with midfrontal theta power (4-8Hz), originating in the medial prefrontal cortex (mPFC). MPFC theta power modulations have been associated with encoding and retrieval processes in LTM and maintenance during WM¹⁵, possibly through functional connectivity with medial temporal lobe (MTL) and hippocampal structures (and see ¹⁶ for a review).

In our paradigm, we aimed to investigate whether a parietal-to-midfrontal shift in neural correlates can be observed when the repeatedly memorized stimulus is not a single search target, but a complex colour-array, which needs to be recollected *explicitly* during the task. In our design, the array consisted of more coloured items than can generally be held in working memory, of which one was probed by spatial location during each trial. The array was therefore more akin to an abstract visual scene, which had to be remembered as a whole, rather than a collection of separate targets. However, we expected that initially, participants would encode the coloured items as separate targets in visual working memory, with a gradual transition to a

coherent representation of the whole array, which would rely more on LTM sustaining structures.

As in the visual search study ¹, we used the CDA component to trace the working memory representation, while the modulation of the midfrontal P170 component was taken as a potential neural signature of memory consolidation within an LTM-supporting system. Bilateral arrays of 6 coloured squares each, were repeatedly presented during a testing block of 8 trials, with one hemifield being cued for covert attention at the beginning of the testing block. In each trial, the colour of one of the squares in the array was probed following a 2.5 second delay, with a combined central colour- and a peripheral spatial-cue highlighting one of the array-squares ('memory cue'). This way, participants had to construct an explicit mental representation of the colour-array's spatial lay-out during each trial in order to perform the task. Importantly, the item-set-size exceeded the visual WM capacity limit, which we expected to require stronger recruitment of LTM (MTL/hippocampal) structures (see ⁵).

During the main experiment, parietal contralateral activity- and midfrontal-responses were measured during the early learning- (trial 1-4) and late learning phase (trial 5-8) of the WM blocks. These components were measured from array onset throughout the delay, relative to the ERP in a control attention (ATT) condition, during which the cue was presented simultaneously with the colour-array. The same components were also measured during recollection of the memorized array after the delay, probed by the memory cue in the WM condition. With respect to the parietal component, we refer to contralateral activity (CA) while the array or memory-cue is present on screen and contralateral *delay* activity (CDA) during the WM delay following array-offset.

Memory consolidation was assessed in a subsequent post-hoc old/novel recognition task. The midfrontal P170 response to old- and novel colour-arrays was measured, to assess lasting neural modulation accompanying the longer-term perceptual memory consolidation ¹⁰.

During the main experiment, we expected a gradual decline of a WM-delay-specific CDA component (and no contralateral activity (CA) present in the ATT condition) when learning progressed. Conversely, we expected an increasingly enhanced negative modulation of the midfrontal component during the learning process^{2,3}. We further predicted a more prominent parietal component during gradually more successful (explicit) recollection of the colour-array following the cue ³⁰⁻³⁸. Furthermore, we hypothesized that, if the midfrontal response modulation signaled transfer of the memorandum from a working- to another longer-term memory store during the main experiment, this modulation should be predictive of accuracy in a post-hoc recognition task. Finally, longer-term perceptual memory during the recognition task should be visible as a lasting neural modulation of the midfrontal P170 response upon re-exposure to old colour-arrays ^{14,17}.

2. Materials & Methods

2.1 Participants

Twenty right-handed healthy volunteers (sample size based on an expected change in the CDA difference wave of $\sim 1.5\mu\text{V}$; with desired power of 90%) with normal (or correct-to-normal) vision, were recruited to take part in the experiment (11 female; age 25,5 $\pm$ 6) and were financially reimbursed for their time. All participants provided informed consent and all experimental methods conformed to the ethical principles of the Declaration of Helsinki and were approved by the Ethics Committee of the Faculty of Social and Behavioural Sciences of Utrecht University.

For the main experiment, all participants were included in the behavioural analysis and one participant had to be excluded from EEG analysis, due to excessive artefacts (see for criteria below). For the follow-up recognition task, the first 6 participants had to be excluded from analysis due to a technical error. Both behavioural- and ERP analysis for this part of the experiment were performed on the remaining 14 participants.

2.2 Behavioural Task

The experiment consisted out of 2 parts, the main experiment and a subsequent recognition task. A schematic representation of the experimental paradigm during the main experiment is shown in Fig. 1. Task (Working Memory (WM)/Attention (ATT)) was manipulated within participants across 8-trial blocks. At the beginning of each testing block, a central arrow indicated which hemifield to attend to during the subsequent 8 trials and would remain visible throughout the duration of the testing block. After 750 ms following spatial cue onset, 2 different arrays, each consisting of 6 coloured squares at fixed locations, were bilaterally presented (750 ms), followed by a scrambled colour mask (250ms). This was an initial presentation of the colour-array-combination that was subsequently repeated in the ensuing

8 trials. A trial would start with a slight brightening of the central fixation square (750ms). During each trial, participants had to match a central colour probe with the colour at one square in the array, highlighted by a black rectangle around it. This combined cue (central colour and peripheral rectangle) was presented for 750ms, either while the array was still present on screen (ATT block) or following a 2.5 second delay (WM block). Locations of all squares in the bilateral arrays and at central fixation remained visible as white placeholders at all time when the colour-array was not on screen. ITI intervals were 2.5 seconds for both conditions. Participants were encouraged to maintain a visual memory of the cued colour-array during the delay periods of the WM condition.

Participants responded with their right hand by using self-chosen keys on a keyboard for “match” or “no-match”. The central colour cue had to be the same as the colour *at the highlighted location* in the array to be deemed a match (50% of trials) and was considered a non-match when the colour was not present in the array at all (25% of trials) or present but not at the highlighted location (25% of trials). The task was non-speeded and participants were instructed to respond as accurately as possible.

Task (ATT or WM) and attended hemifield were randomized across testing blocks. Three match-conditions (match (colour *and* location), no-location-match and no-colour-match) were pseudo-randomized across trials, with a 50/25/25 % chance distribution for each condition across each trial position (1-8) within a testing block. Each participant performed 6 separate sessions, comprising 6 testing blocks of 8 trials, with 288 trials in total.

Stimuli were generated on a Dell computer (Dell, Round Rock, TX, USA) and presented on a LG 24MB65PM LCD monitor (2560 x 1440 pixel spatial resolution and 100 Hz refresh rate), using Matlab (Mathworks, Natick, MA, USA; version: R2016a), Cogent 2000 (developed by the Cogent 2000 team at the WCHN and the ICN, London) and Cogent Graphics (developed

by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience, London). The size of the screen was 50.8×33.9 cm. The 6 different colours allocated to each square of an array were randomly drawn (separately for each hemifield) from a pool of 8 highly discriminable but equi-luminant colours (red, gray, brown, green, purple, turquoise, orange and pink (24.5 ± 2.5 cd/m²). Arrays were presented on a gray background (72 cd/m²). Squares in the arrays subtended 0.75° in visual angle each with 2 squares presented in 3 rows, with 1° vertical distance between squares (center to center) and 3° horizontal distance between squares in the upper and the lower row and 1° horizontal distance between squares in the middle row. Centre of the arrays were presented 4.5° from fixation. Preceding onset of the EEG experiment, participants completed 2 practice blocks of each task condition. During the EEG experiment, lights were switched off, while participants were seated in a comfortable chair, 66 cm from the monitor with their heads resting on a desk-mounted chinrest. They were instructed to maintain fixation on a central square in the middle of the monitor array, while covertly attending the cued hemifield throughout each testing block. Adhered fixation was monitored with an Eyelink1000 eyetracker (SR Research). Participants were instructed to refrain from blinking as much as possible until the 5 second breaks in between testing-blocks. Following a ca. 5 minute break after completion of the main experiment, during which participants remained seated and attached to the EEG apparatus, the post-hoc recognition task would commence. Participants were not informed about this task until after they had completed the main experiment. For this task, all colour-arrays that had been presented during the main experiment in the attended hemifield (either during ATT- or WM blocks) were randomly intermixed with novel array configurations made up out of the same colour pool. In total there were 72 trials, of which 36 contained novel- and 36 contained old arrays (18 presented during either condition (ATT/WM)). Note that due to randomization of all trials, there was on average

an interval of ca. 35 minutes between initial array-exposure during the main experiment and the test probe during the post-hoc recognition task. A trial would commence with a slight brightening of the central fixation square (500 ms), followed by a central presentation of a colour-array (2000 ms), with an equiprobable chance to be drawn from the ‘old’- or ‘novel’ set. Participants were asked to indicate whether they recognized the presented colour-array and instructed to respond ‘yes’ when they felt more than 60% confident. Responses had to be indicated with their right hand by pressing either of two self-chosen keys on the keyboard. Participants were instructed to withhold their responses until offset of the colour-array and to be as accurate, not as fast as possible. The following trial started after a 3.5 second inter-trial-interval, during which a white square would remain visible at fixation.

208 2.3 Behavioural data analysis

209 *2.3.1 Main Experiment*

210

211 Behavioural measures, including accuracy scores (d' scores¹⁸ during the EEG experiment) and
212 RTs were each analyzed by a repeated measures ANOVA with two factors: Task (Attention/
213 WM) and Trial Group (first four trials/ second four trials). As it was a non-speeded task,
214 accuracy scores were our main measure of interest.

215

216 *2.3.2 Post-hoc recognition task*

217 Sensitivity scores for old/novel discrimination (d' score; ¹⁸) were calculated for the post-hoc
218 recognition task. The d' score was calculated using the following equation: $d' = Z(\text{hit rate}) - Z$
219 $(\text{false alarm rate})$.

220 Initially d' scores were calculated including all 'old' array trials, irrespective whether they had
221 been presented during the ATT or WM condition during the main experiment and in a
222 subsequent analysis, d' scores were calculated separately for old arrays that had been presented
223 during the ATT or WM condition.

224

2.4 Eyetracking

Saccades were detected offline with the default values of the EyeLink algorithm for saccade detection applied across trial segments restricted to the stimulus duration (either 2000 ms following colour-array onset or 1000 ms following memory-cue onset). Trials with saccades during the selected time segments were excluded from further analysis.

Average fixation was within 1.5 degrees from fixation for all participants in all conditions (see Supplementary Fig. S3). Across participants, a slight hemifield bias was observed during the first four trials of the WM condition and not in any other condition (Interaction Task x Trial Group x Hemifield $F(1,18)=7$ $p=.02$). However, this bias was only minor ($<.3^\circ$; see Supplementary Fig. S3e) and we do not expect that this had any substantial impact on the results.

2.5 EEG Recording

The EEG was recorded continuously using a 64-channel Biosemi amplifier system with electrodes positioned according to the 10–20 international system (AEEGS, 1991). Separate electrodes were placed on the supraorbital and infraorbital ridges of the left eye and on the outer canthi of the right- and left eyes to calculate EOG signals for blink- and eye-movement artifact detection.

During EEG recording, electrode impedances were kept below 20 k Ω . Each electrode was measured on-line with respect to the CMS/DRL electrodes producing a monopolar channel. The ongoing brain activity at each electrode site was sampled using the ActiView application at 2048 Hz and filtered with a low-pass filter of 100 Hz, and a high-pass filter of 0.16 Hz.

2.6 EEG Processing

EEG data were analyzed in MatLab using SPM and FieldTrip^{19,48} software. The data were re-referenced off-line to the algebraic average across all electrodes and then low-pass filtered (40 Hz) to exclude high-frequency noise and high-pass filtered (0.1 Hz) to eliminate slow drift (1 Hz for the post-hoc recognition experiment).

The continuous EEG was then segmented into epochs, time-locked to the onsets of the colour-array. Epochs were 3700-ms long, beginning 200 ms before array-onset and ending after 3500 ms, just before either the onset of the following trial (ATT condition) or presentation-onset of the memory-probe (WM condition). The segment containing the response to the memory probe was epoched separately, starting 200 ms before cue-onset and ending 1200 ms later, 250 ms post cue-offset. The pre-stimulus baseline of 200 ms was used for all analyses.

Data quality was initially inspected using automated algorithms. Epochs containing excessive noise or drift ($\pm 80 \mu\text{V}$) at any electrode were marked and channels in which more than 20% of the epochs were affected were excluded. One participant was excluded, of whom more than 20% of the channels was deemed bad according to these criteria. Blinks were identified as large deflections ($\pm 4 \times \text{SD}$) in the VEOG signal (subtraction of the signal from the EOG electrodes above and below the left eye) and were marked. All marked artefacts were later accounted for during robust averaging. Epochs were averaged according to task (ATT/WM), trial group (first four trials/second four trials) and attended visual hemifield.

2.7 EEG Analysis

2.7.1 Main experiment

For the C(D)A analysis, ERPs were averaged across the PO7/O1 electrodes (left hemisphere) and PO8/O2 electrodes (right hemisphere). ERPs were subsequently combined across trials by an averaging procedure that preserves the electrode location relative to the attended hemifield (contra- or ipsilateral) ^{4,6,20}. Previous studies investigating CDA generally studied relatively short delay intervals (ca 300-1000ms following stimulus onset, see ^{1,2,4,6}). We therefore limited our analysis for these previously reported time-windows. Since stimulus presentation was longer in our paradigm (compared to previous studies) only the first 300ms post colour array-offset was included (reflecting true delay-activity) into our first analysis. Mean amplitudes of the difference waves between contra- and ipsilateral delay activity were computed during this 800-1100ms time-window.

The mid-frontal component was computed by averaging ERPs across 4 mid-frontal electrodes (aFz, Fz, F1 and F2) and mean amplitudes were calculated during the peak response following array onset (P170, see ^{2,10}) and during the 300ms post array-offset.

During memory-cue presentation, parietal CA was measured from the moment it emerged (350 ms following cue onset ^{4,6,7}) until 100 ms pre cue-offset. The P170 component was measured during the peak 170ms following cue-onset.

Two-way repeated measures ANOVA were conducted for the mean amplitudes, testing the effects of Task and Trial-group. To test whether individual differences in measured signals

predicted WM and/or recognition task performance, Robust Pearson correlations were computed between mean amplitude and task performance (d'). We performed this correlation analysis not only averaged across the 300ms time-window, but specifically also for a longer time into the WM delay (1000ms following array-offset).

The percentage bend correlation is a robust method that protects against outliers among the marginal distributions. (Matlab Corr_toolbox 2012; Cyril Pernet and Guillaume Rousselet 2011-2011). Trimming percentage, ie. negative weighting of outliers, was set to default (20%).

The Greenhouse–Geisser epsilon correction for nonsphericity was applied to all ERP analyses where appropriate²¹, and only corrected probability values and degrees of freedom are reported.

312 2.7.2 *Post-hoc recognition task*

313

314 The analysis of the post-hoc recognition task aimed to test longer-term perceptual priming and
315 measured a potential modulation of the midfrontal P170 response to repeated (old) arrays
316 compared to non-repeated (novel) arrays¹⁰ .

317

3. Results

To test whether a learning-associated shift in visual WM correlates could be observed during repeated encoding and recollection of a multi-item colour-array, we conducted an EEG experiment using a visual WM paradigm as depicted in Fig. 1 (and see Methods). This was followed by an array-recognition task to test whether observed modulation of neural correlates during the WM task facilitated longer-term consolidation.

Fig. 1 Schematic representation of the task.

Two different arrays, consisting out of six coloured spatially-fixed squares each, are bilaterally presented with one hemifield cued for covert attention at the beginning of (and throughout) a testing block. The same array-combination was repeated for 8 trials in one testing block and spatial locations of all squares would remain visible as white placeholders during stimulus intervals. Participants had to match a central colour cue with that at one highlighted square in the array, either while the colour-array was still present on screen (attention/ATT condition, left) or following a 2.5 second delay (WM condition, right).

327

328 In a previous pilot experiment we had shown that gradual learning of the colour-array
329 configuration reached a plateau performance after ca. 8 trials (see Supplementary Fig. S1b).
330 Moreover, the array-recognition task in this pilot experiment confirmed longer-term memory
331 consolidation, in particular for colour-arrays presented during the WM- as compared to the ATT
332 condition (see Supplementary Fig. S1c). In a second pilot experiment, we tested the hypothesis
333 that a set size exceeding the visual WM capacity-limit (6) would enhance the reliance on a
334 longer-term memory-supporting storage system for holding a mental representation online
335 during visual WM, which should be reflected in a stronger memory consolidation. We found
336 indeed support for this hypothesis, as 6-item arrays were better remembered in a post-hoc
337 recognition task than 4-item arrays (see Supplementary Fig. S2).

338

339

3.1.1. Behavioural performance during the EEG experiment (WM task)

Guided by the pilot findings, 6-item colour-arrays were used in the EEG experiment, which were repeated during 8-trial blocks. A similar gradual increase in accuracy-scores over trials was observed in the EEG experiment, as had been shown for 6-item arrays in the second pilot experiment (see Fig. 2A and Supplementary Fig. S2). For statistical analysis of task performance, accuracy scores (d') were collapsed across the first- and the second four trials separately and an ANOVA was applied with Trial-group (first four trials/second four trials) and Task (ATT/WM) as factors. As shown in Fig. 2b, the gradual increase in performance during the WM condition was reflected in a significant difference between trial-groups, while no significant change was detected during the ATT condition (Main effect Task $F(1,19)=19$ $p<.001$; Main effect Trial Group $F(1,19)=25.3$ $p<.001$; Interaction Task $\times$ Trial-group $F(1,19)=15.6$ $p=.001$; pairwise comparison between trial-groups for the WM condition $T(1,19)=-5.1$ $p<.001$ and for the ATT condition $T(1,19)= -1.7$ $p=.103$ ns.). This observed increase in accuracy scores for the WM condition did not coincide with faster reaction times (see Supplementary Fig. S4).

a.

b.

Fig. 2 WM task accuracy scores.

a.) Mean d' scores during the ATT and WM condition are plotted for 8 consecutive trials in a testing block. A gradual increase in accuracy during the WM condition reached a plateau around the fifth trial, while performance for the ATT condition was around ceiling throughout the testing block. b.) Plotted are the accuracy scores for both conditions, averaged across the first- and the second four trials.

357

358 As outlined before, we expected that this gradual learning across trials in the WM condition
359 would be accompanied with a parietal-to-midfrontal shift in neural correlates during the
360 memory delay period ^{1,2}. Specifically, we predicted that a parietal CDA component would be
361 most prominent during the first four trials (early learning), when we expect the coloured squares
362 to be held as separate targets in working memory. This should decline when learning progresses
363 and a more profound modulation of the midfrontal component was expected to emerge during
364 the second four trials (late learning), presumably signaling a transfer to an LTM-supporting
365 storage system.

366

3.1.2. Behavioural performance during the EEG experiment (recognition task)

The main task was followed by a post-hoc recognition task, during which all colour-arrays that had previously been presented in the attended hemifield during the main task (ATT- or WM condition) were shown again, randomly intermixed with novel array configurations, made up out of the same colour pool. Participants had to indicate whether they recognized the presented arrays with a confidence higher than 60%.

As observed in the behavioural pilot experiments preceding the EEG study, the repeated exposure to the colour-arrays resulted in a positive d' score during the post-hoc recognition task as plotted in Fig. 3a (mean d' -score=0,32; $T(13)=6,73$ $p<.001$). Unlike during the first pilot experiment (see Supplementary Fig. S1c), no significant difference was detected between d' recognition scores for arrays shown during the ATT- versus the WM condition (Fig. 3b; pairwise comparison $T(13)=-.53$ $p=.6$ ns.). It should be noted however, that during the earlier behavioural pilot, experimental conditions were slightly different and had more trials per block (see discussion). However, also with 8 trials per test-block in the EEG session, we observe a modest but significant above chance d' score across conditions in the recognition task, indicating longer-term consolidation across conditions.

Fig. 3 Recognition task accuracy scores.

Accuracy scores on the post-hoc recognition task are plotted as d' scores across conditions (a) and separated for colour-arrays that had previously been shown during the ATT or the WM condition (b).

3.2 EEG analysis: Encoding and maintenance during the visual WM task

3.2.1 Parietal contralateral activity

First, the parietal contralateral response was measured from colour-array onset (Contralateral Activity, CA) and throughout the memory delay or ITI (Contralateral Delay Activity, CDA) per task condition (ATT/WM) and trial-group (first four trials/second four trials). This response was plotted as difference waves between contra- and ipsilateral activity across occipital-parietal electrodes (see Fig. 4a-b). As can be seen in Fig. 4a, a C(D)A component was visible for the WM condition, starting around 300 ms post array-onset and persisting during a short time into the delay period during early learning (first four trials).

As a CDA component was only detectable for a relatively short time during the delay, even during the early learning trials, we calculated mean amplitudes during a selected time-window of 300 ms following array offset (plotted in Fig. 4c; see also methods) and compared these between both trial groups to test our prediction of a learning-associated decline in the CDA. An ANOVA, including the factors Task and Trial-group, revealed a significant Task x Trial-group interaction for this time-window (interaction Task x Trial-group $F(1,18)=4.7$ $p=.045$; pairwise comparison Task for first four trials $T(18)=2.76$ $p=.013$; pairwise comparison Task for second four trials $T(18)=.13$ $p=.9$ ns.). In other words and in line with the prediction: while a WM-specific CDA component was present for 300ms following array-offset during early learning (first four trials), it had disappeared during late learning (second four trials). It has to be noted here that for the late learning trials, a Contralateral Activity (CA) was still visible during array presentation. Qualitatively, the decrease in strength of the C(D)A component when learning progressed, seems therefore to reflect a narrowing of the response for late learning trials to a short time-window during array presentation.

411 In summary, we do observe a learning-related decline in the WM-specific parietal C(D)A
 412 response following array onset. However, even in the early learning phase (first four trials), this
 413 component is only visible (averaged across participants) for a relatively brief time into the WM
 414 delay period. Note that the signal was corrected for saccades and blinks up till 1 second post
 415 array-offset, which may account for a noisier signal later during the delay.

416 To test whether the CDA may have become less prominent due to variable responses between
 417 participants, but still sustains WM maintenance for a longer time into the delay, we performed
 418 a second analysis in which we correlated responses with task performance per participant. CDA
 419 mean amplitudes were averaged across a longer time into the WM delay (1 second) and
 420 correlated with task accuracy (d') during the WM task. To test whether the CDA response
 421 during the delay had any relevance for longer term memory consolidation we performed an
 422 additional correlation analysis with task accuracy (d') during the subsequent recognition task.

423 No significant correlation was found between the CDA mean amplitudes and WM (d')
 424 performance (see Fig. 4 h-i; first four trials: $R=0.10$; $T=0.41$; $p=0.68$ ns.; second four trials:
 425 $R=0.11$ $T=0.47$ $p=0.64$ ns.). In contrast, a significant correlation was observed between the
 426 CDA mean amplitudes during the first 4 trials of the WM task and subsequent performance (d')
 427 during the later recognition task (see Fig. 4l; $R=-0.57$ $T=-2.31$ $p=0.04$), which was not observed
 428 for the mean CDA amplitude during the second 4 trials (Fig. 4m; $R=0.11$ $T=0.36$ $p=0.72$ ns;
 429 Williams's test between correlations $T(12)=2.18$ $p=.05$). Also for the short time-window post
 430 array-offset (800-1100ms), no significant CDA-behaviour correlations were observed with
 431 WM accuracy ($p>.6$ ns.), but a similar significant correlation was observed with recognition
 432 accuracy for the CDA amplitude during the first 4 trials ($R=-0.65$; $T=-2.87$; $p=0.015$). No
 433 significant activity-behaviour correlations were observed for the ATT condition ($p>.35$ ns.).

434 The CDA response therefore does not seem to reflect visual WM maintenance throughout the
 435 delay, but may reflect a non-sufficient contribution to memory-maintenance, ie. keeping only a

subset of the coloured squares in mind, during early learning trials. Furthermore, our results suggest that the C(D)A also supports a (longer-term) encoding mechanism.

3.2.2. Midfrontal response

We next tested whether learning of the colour-arrays in the WM condition concurred with a negative modulation of the midfrontal component, which is associated with long-term perceptual priming¹. The midfrontal component was averaged across four electrodes (AFz, Fz, F2 and F3) per task-condition (averaged across hemifield) and per trial-group, and plotted from array-onset throughout the WM delay (see Fig. 4d), as well as for the first 350 ms following array-onset separately to visualize the P170 peak (see Fig. 4e). Mean amplitudes were calculated for all four conditions for the P170 peak (see Fig. 4f) and, as for the CDA analysis, also for the 300 ms time-window post array-offset (see Fig. 4g).

An ANOVA, including the factors Task and Trial-group, revealed a main effect of task for the P170 component, with a smaller amplitude during the WM- as compared to the ATT condition ($F(1,18)= 24.99$; $p<.001$; see Fig. 4f). The negative modulation of the P170 peak for the WM condition became more pronounced when learning progressed, as compared to the ATT condition. This was reflected in a significant Task x Trial-group interaction, with a enhanced difference between WM and ATT for the second 4 trials compared to the first 4 trials (Task x Trial-group interaction: $F(1,18)= 4.37$; $p=0.05$; Pairwise comparison Trial 1-4: $T(18)=.32$; $p=0.75$ ns.; Trial 5-8: $T(18)=3.74$; $p=.002$). Mean amplitudes during the 300ms time-window post array-offset are shown in Fig. 3g, but note that direct comparison between the task conditions is problematic, since the ATT condition required a button-press immediately following array-offset (this confound is canceled out in the difference potential of the CDA, but not for the MF analysis). The effect of interest here is the pairwise comparison between the

first- and second 4 trials of the WM condition, which did not reach significance ($T(18)=1,27$ $p=.22$), possibly due to high inter-subject variability in the signal.

We subsequently performed a robust correlation analysis for the WM condition only, to investigate whether inter-subject variability in the midfrontal response modulation during the delay had any predictive value for WM task-performance (and hence any functional relevance). As for the CDA component, the mean amplitude of the midfrontal signal was averaged during the first second of the delay for each participant per trial group and correlated with individual WM performance (see Fig. 4j-k). This analysis revealed a significant negative EEG-behaviour (d') correlation for the second 4 trials ($R(19)= -0,52$; $T=-2,50$; $p=0,023$; Fig. 4j) and surprisingly, a positive correlation was observed during the first 4 trials ($R(19)= 0,46$; $T=2,11$; $p= 0,05$; Fig. 4i ; Steiger's test between correlations $z(18)=3,01$ $p<.05$). These findings suggest a functional relevance for visual WM maintenance of the observed sustained midfrontal modulation.

To test whether the modulation of the midfrontal component during the WM delay phase was predictive for longer-term consolidation (and hence indicative of the recruitment of an LTM supporting system) correlations with performance (d') on the posthoc recognition-task (d') were performed. We indeed observed significant correlations between the WM delay midfrontal mean amplitude and post-hoc recognition task d' (see Fig. 4n-o; first four trials: $R(19)= 0,57$; $T=2,32$; $p=0.04$; second four trials: $R(19)= -0,62$; $T=-2,65$ $p=0.022$), with again a difference between early- and late learning trials (Williams test between correlations $t(12)=-3$; $p<.05$).

Similar but not always significant correlations were observed for the short 300ms segment post array-offset (EEG-WM d' first 4 trials: $R(19)= 0,3$; $T=1,3$; $p=0,21$; second four trials: $R(19)= -0,57$; $T=-2,85$ $p=0,01$; EEG-LTM d' : first 4 trials: $R(19)= 0,55$; $T= 2,2$; $p=0,05$; second 4 trials: $R(19)= -0,53$; $T=-2,08$; $p=0,06$).

No significant activity-behaviour correlations were observed for the P170 peak ($p>.25$ ns.).

Fig. 4 Parietal contralateral activity and midfrontal response during encoding and WM maintenance.

Upper panel: C(D)A components are plotted as difference waves between contra- and ipsilateral activity per task-condition (ATT/WM), from the moment of colour-array onset and throughout 2000ms of the WM delay period during the first four trials (a) and the second four trials (b). The mean amplitudes of the C(D)A difference waves are plotted per task-condition and trial-group, as calculated during a 300 ms time-window immediately following array-offset (c) (time-window indicated as filled gray box in a and b).

Second panel: Plotted are the midfrontal responses for all 4 task conditions from colour-array onset throughout the delay period (d.) and for the midfrontal P170 peak specifically during 350 ms following colour-array onset s (e). Mean amplitudes per task-condition and trial-group were calculated and plotted for the P170 peak (f; time-point indicated as gray line in e) and also for the 300 ms time-window post array-offset (g).

Lower panels: Correlations are shown between mean amplitudes (CDA and midfrontal responses), calculated across the first 1000ms of the WM-delay following array-offset (indicated by open gray box in a, b and d) and d' accuracy scores during the WM task (CDA: h,i; midfrontal: j,k) and the posthoc recognition task (CDA:l,m; midfrontal:n,o).

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3.3 EEG analysis: Explicit recollection during the visual WM task

Next, we assessed learning-associated changes in the parietal CA-response and the midfrontal P170 component during explicit recollection of the learned colour-array, as probed by the memory-cue in the WM condition following the 2500ms delay.

As can be seen in Fig. 5a, a memory-cue-induced CA component is not present during early learning (first four trials), but emerges during late learning (pairwise comparison Trial-group: $T(18) = 2.2$; $p = 0.04$). For the midfrontal P170 peak (see Fig. 5b), no significant learning-associated effect was observed ($T(18) = .29$; $p = 0.77$ ns.).

Fig. 5 Parietal contralateral activity and midfrontal response during WM recollection.

Plotted are the parietal CA difference waves (a) and midfrontal P170 responses (b) for both trial groups during explicit recollection of the memorized colour-array, as probed by the memory cue following the WM delay (t_0 =memory-cue onset). Mean CA amplitudes are calculated during a 300ms time-window while the cue was on screen (b; time-window indicated as filled gray box for CA in a) and for the midfrontal P170 peak after cue-onset (d; time-window indicated as as gray line for P170 peak in c).

3.4 EEG analysis: Reflection of longer-term visual memory consolidation in the modulation of the midfrontal response during the recognition task.

In line with our predictions based on previous studies^{1,2}, we observed a WM-specific modulation of the midfrontal P170 component, which became more pronounced with learning. While we did not find a direct link with task-performance for modulation of the P170 peak, we did observe a significant correlation between a sustained negative modulation of the midfrontal component during the WM delay and WM accuracy, when learning progressed. These findings imply a functional significance of this modulation for visual WM maintenance. Furthermore, we provide supporting evidence indicating that the sustained midfrontal response modulation reflects recruitment of an LTM-facilitating system, as significant correlations were also present between this activity and performance accuracy during the subsequent recognition task. To investigate whether perceptual memory consolidation was manifested as modulation of the midfrontal P170 response upon re-exposure to the colour-arrays¹⁰, the EEG signal was measured while participants were performing the post-hoc recognition task. Fig. 6(a) shows the midfrontal response to the presented colour-arrays for correct trials, separated for repetition (old/novel). Pairwise comparison revealed a greater P170 mean amplitude for repeated (old) colour-arrays compared to novel colour-arrays, indicating a longer-lasting modulation (see Fig. 6b; $T(13) = 2.328$; $p = .037$). No significant difference was observed in P170 response between old arrays that had been presented during the WM condition in the main experiment compared to those during the ATT condition, although a tendency seemed present for a late modulation ($T(13) = -1.33$; $p = 0.21$ ns.; see Supplementary Fig. S5). This was perhaps not surprising, as no significant behavioural difference (in d') was observed between these conditions during the EEG experiment. Of the two repeated colour-array condition, the (late) P170 response to the WM condition was

538 significantly greater than the novel condition ($T(13)= 2.18$; $p= 0.048$) while the ATT condition
539 was not ($T(13)= 0.67$; $p= 0.52ns.$)

Fig. 6 Midfrontal response during the recognition task.

Plotted are the midfrontal responses during the post-hoc recognition task to previously shown (old)- and novel colour-arrays for correct trials (a). Mean amplitudes at 170 ms post array-onset (indicated by gray line in a) are plotted per array-type (old/novel) (b).

4. Discussion

The current study investigated whether the gradual strengthening of an explicit and rich visual memory concurs with a shift of parietal-to-midfrontal neural activity, as was previously shown for the memory of a single visual-search target (probed by the *implicit* memory measure of response speed)^{1,2}. In addition, we also investigated the hypothesis that this shift in neural correlates could signify the recruitment of a longer-term-memory supporting storage system.

Our results reveal a learning-associated decline in parietal CDA during repeated memorizing of a multi-item colour-array. However, even during the early learning phase, the CDA is, on average, only briefly observed and not throughout the whole WM-delay period (of note here is that in previous studies much shorter delay intervals were tested (ca 1000ms))^{1,2,4,6}. This could indicate that maintenance of the memory trace is just briefly and not sufficiently sustained by parietal activity even during these early learning trials. Alternatively, it is possible that the memory representation becomes less lateralized throughout the delay and therefore hard to detect by measuring the CDA.

In addition to this, our results provide clear support for an involvement of this contralateral parietal activity in *encoding* of the colour-array, as a positive EEG-behaviour correlation with performance on the post-hoc recognition task is observed. Qualitatively, the C(D)A narrows in duration when learning progresses and is still (and only) present during array-presentation. This may indicate involvement in a (gradually) more efficient encoding process. As is apparent from the behavioural data, learning had not reached ceiling level after 8 trials and encoding-related activity may therefore reflect ongoing learning. Results from our pilot experiment showed that more trial repetitions (16) significantly enhanced post-hoc recognition and proper consolidation may occur particularly while WM performance is at ceiling. Future study may clarify whether encoding-related CA activity disappears completely during ceiling-performance.

While fronto-parietal regions have been implied in memory-encoding before^{22,23}, our findings suggest that parietal CA reflects a specific mechanism, which can be dissociated from selective

attention (as no CA activity was observed during the attention condition). This mechanism may involve processes that promote LTM by strengthening inter-item associations^{24,25}, and/or spatial binding, possibly through interaction with MTL- and hippocampal structures²⁶⁻²⁹.

Interestingly, whereas the CDA component gradually decreases during the WM-delay, a learning-associated CA component slowly emerges during successful *recollection* of the memorized colour-array, prompted by the combined colour-spatial cue following the WM-delay. This is in line with previous reports of a late parietal component during memory recollection¹³. As Rugg et al demonstrated and corroborated by multiple studies since, this late parietal component is specifically observed during *explicit, vivid recollection* of a memorandum³⁰⁻³⁹. It could be speculated that the observed parietal CA in our study, may serve to bring visual information in a privileged (stable) mental state or buffer⁴⁰, initially to facilitate encoding (and insufficient maintenance) of visual input and subsequently to visualize the detailed, spatial context of the memorized information during recollection. The sustained parietal activity during these processes may facilitate information transfer to (and from) MTL regions^{5,41-43}.

Our experimental paradigm was deliberately designed to promote this interaction with MTL-hippocampal regions. We expected that the combination of a beyond-WM-capacity-set-size and the spatial context of our task, would enhance reliance on MTL-hippocampal structures (see⁸). Due to the large set size, we expected that the memory trace could not be sustained by parietal visual WM mechanisms alone and that an extended memory network would need to be recruited. It seems indeed the case that the parietal CDA response did not sustain the visual memory sufficiently and we observed a WM-specific modulation of the midfrontal P170 component (compared to the attention condition), which became more prominent as learning progressed. This modulation is similar to what was described before in the repeated search

paradigm^{1,2} which was interpreted as a transfer of the memorandum (search target) to an LTM storage system. This interpretation was motivated by previous studies which demonstrated modulation of this component during long-term perceptual memory priming processes¹⁰. In our task we do not observe a significant correlation between modulation of the P170 component and task-accuracy. However, we find that the level of negative modulation of the midfrontal response during the delay period is predictive for WM accuracy when learning progresses (and a transition from WM to short-term memory occurs). This is an indication that *sustained modulation* of midfrontal activity is involved in maintaining the memory trace during the WM delay.

In addition, the averaged midfrontal component during WM-delay correlated with performance accuracy in the subsequent post-hoc recognition task. This suggests that the sustained modulation of the midfrontal component reflects recruitment of an LTM-supporting system^{1,2} which contributes to WM-maintenance during the delay phase.

Surprisingly, we observe a positive EEG-behaviour correlation during early learning trials, both for task accuracy in the WM- and the post-hoc recognition task. Perhaps midfrontal activity subserves different underlying mechanisms and memory is first actively consolidated during early learning trials, while merely protected from interference during late learning trials.

The source of the midfrontal activity may be the ventromedial prefrontal cortex, which has been implicated in memory encoding by multiple studies⁴⁴⁻⁴⁶ (and see⁴⁷ for a review). The nature of the signal remains unclear but further analysis could clarify a potential link with midfrontal theta oscillations, which have been associated with maintenance during working memory¹⁵ and information-transfer to MTL/hippocampal regions during encoding- and retrieval processes in long-term memory (and see¹⁶ for a review). Modulation of the P170 peak might reflect a

memory-specific phase-reset mechanism of midfrontal theta-oscillations, which prepares the system for memory encoding ¹⁵.

Finally, we not only observed visual memory consolidation on the behavioural level, but also observed lasting influences on the midfrontal response upon re-exposure to the previously presented colour-arrays during the recognition task. A modulation in the P170 peak was observed during trials in which colour-arrays were correctly recognized as old or novel. This further supports the notion that the P170 modulation during the WM task is indicative of the formation of a longer-term memory trace.

5. Conclusion

In conclusion, the present study provides evidence for the recruitment of an LTM-supporting system when a visual image is repeatedly held in working memory. This is indexed by modulation of a midfrontal component during encoding and maintenance and is accompanied by the emergence of a parietal CA during gradually enhanced recollection. In contrast, there is a gradual decline of parietal C(D)A following array presentation, which may partly reflect an decreased (insufficient) contribution to WM maintenance, but seems more related to LTM encoding.

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Acknowledgements:

The authors would like to thank Milena Engel and Lucia Zemene for behavioural data collection. This work was supported by The Netherlands Organization for Scientific Research Vidi Grant 452-13-008 (to S.V.d.S.)

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779 **Supplementary information:**

780 Supplementary data to this article can be found online at:

781

782 **Additional Information:**

783

784 **Competing Interests:** The authors declare that they have no competing interests.

785

786 **Data availability statement:**

787 The datasets generated during and/or analysed during the current study are not publicly
788 available due to ongoing analysis for a follow-up study, but are available from the
789 corresponding author on reasonable request.

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Figures

Figure 1

Schematic representation of the task. Two different arrays, consisting out of six coloured spatially-fixed squares each, are bilaterally presented with one hemifield cued for covert attention at the beginning of (and throughout) a testing block. The same array-combination was repeated for 8 trials in one testing block and spatial locations of all squares would remain visible as white placeholders during stimulus intervals. Participants had to match a central colour cue with that at one highlighted square in the array, either while the colour-array was still present on screen (attention/ATT condition, left) or following a 2.5 second delay (WM condition, right).

a.

b.

Figure 2

WM task accuracy scores. a.) Mean d' scores during the ATT and WM condition are plotted for 8 consecutive trials in a testing block. A gradual increase in accuracy during the WM condition reached a plateau around the fifth trial, while performance for the ATT condition was around ceiling throughout the testing block. b.) Plotted are the accuracy scores for both conditions, averaged across the first- and the second four trials.

Figure 3

Recognition task accuracy scores. Accuracy scores on the post-hoc recognition task are plotted as d' scores across conditions (a) and separated for colour-arrays that had previously been shown during the ATT or the WM condition (b).

Figure 4

Parietal contralateral activity and midfrontal response during encoding and WM maintenance. Upper panel: C(D)A components are plotted as difference waves between contra- and ipsilateral activity per task-condition (ATT/WM), from the moment of colour-array onset and throughout 2000ms of the WM delay period during the first four trials (a) and the second four trials (b). The mean amplitudes of the C(D)A difference waves are plotted per task-condition and trial-group, as calculated during a 300 ms time-

window immediately following array-offset (c) (time-window indicated as filled gray box in a and b). Second panel: Plotted are the midfrontal responses for all 4 task conditions from colour-array onset throughout the delay period (d.) and for the midfrontal P170 peak specifically during 350 ms following colour-array onset s (e). Mean amplitudes per task-condition and trial-group were calculated and plotted for the P170 peak (f; time-point indicated as gray line in e) and also for the 300 ms time-window post array-offset (g). Lower panels: Correlations are shown between mean amplitudes (CDA and midfrontal responses), calculated across the first 1000ms of the WM-delay following array-offset (indicated by open gray box in a, b and d) and d' accuracy scores during the WM task (CDA: h,i; midfrontal: j,k) and the posthoc recognition task (CDA:l,m; midfrontal:n,o).

Figure 5

Parietal contralateral activity and midfrontal response during WM recollection. Plotted are the parietal CA difference waves (a) and midfrontal P170 responses (b) for both trial groups during explicit recollection

of the memorized colour-array, as probed by the memory cue following the WM delay (t_0 =memory-cue onset). Mean CA amplitudes are calculated during a 300ms time-window while the cue was on screen (b; time-window indicated as filled gray box for CA in a) and for the midfrontal P170 peak after cue-onset (d; time-window indicated as as gray line for P170 peak in c).

Figure 6

Midfrontal response during the recognition task. Plotted are the midfrontal responses during the post-hoc recognition task to previously shown (old)- and novel colour-arrays for correct trials (a). Mean amplitudes at 170 ms post array-onset (indicated by gray line in a) are plotted per array-type (old/novel) (b).

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