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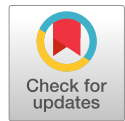
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The Neural Mechanism Underlying Visual Working Memory Training and Its Limited Transfer Effect

Ying Cai¹, Can Yang¹, Sisi Wang², and Gui Xue²

Abstract

■ Visual working memory (VWM) training has been shown to improve performance in trained tasks with limited transfer to untrained tasks. The neural mechanism underlying this limited transfer remains unknown. In the present study, this issue was addressed by combining model-fitting methods with EEG recordings. Participants were trained on a color delay estimation task for 12 consecutive 1-hr sessions, and the transfer effect was evaluated with an orientation change detection task. The EEG responses during both tasks were collected in a pretraining test, a posttraining test conducted 1 day after training, and a follow-up test conducted 3 months after training. According to our model-fitting results, training significantly improved the capacity but not the

precision of color working memory (WM), and this capacity improvement did not transfer to the orientation change detection task, spatial 2-back task, symmetry span task, or Raven reasoning test. The EEG results revealed that training resulted in a specific and sustained increase in parietal theta power suppression in the color WM task, which reflected individual color WM capacity. In contrast, the increase in parietal-temporal alpha power, which reflected individual orientation WM capacity, did not change with training. Together, these findings suggest that the simultaneous change of stimulus type and task structure would modulate the cognitive and neural substrates of WM tasks and introduce additional constraints for the transfer of WM training. ■

INTRODUCTION

Visual working memory (VWM) is the ability to temporally store and manipulate visual information, with a typical limited capacity of approximately four items (Cowan, 2001). VWM is associated with a variety of higher-level cognitive functions, including fluid intelligence (Yuan, Steedle, Shavelson, Alonzo, & Oppezzo, 2006), and VWM dysfunction is a common symptom of various psychiatric disorders, such as schizophrenia (Lee & Park, 2005; Goldman-Rakic, 1994) and Parkinson's disorder (Lee et al., 2010; Gabrieli, Singh, Stebbins, & Goetz, 1996). Accumulating evidence has suggested that working memory (WM) training could lead to both long-term training effects and transfer effects for similar tasks ("near transfer"; Katz, Shah, & Meyer, 2018; Melby-Lervåg & Hulme, 2016). Thus, VWM training has the potential to be an important interventional strategy in clinical and educational settings.

However, despite these positive features, whether WM training can improve performance on untrained tasks with no common features ("far transfer") remains controversial. Previous studies have reported that WM training has a positive transfer effect on reasoning (Klingberg, Forssberg, & Westerberg, 2002), language skill (Chein & Morrison, 2010), and even fluid intelligence (Jaeggi, Buschkuhl, Jonides, & Perrig, 2008). However, recent studies have argued that these initial positive findings may have been overestimated due to methodological

limitations, such as a lack of a suitable control group or formalized training procedures (Harrison et al., 2013; Redick et al., 2013). Some meta-analysis studies have consistently revealed negligible far transfer effects for WM training (Kassai, Futo, Demetrovics, & Takacs, 2019; Melby-Lervåg, Redick, & Hulme, 2016). In addition, recent studies have suggested limited transfer effects across different WM tasks, for example, from *n*-back tasks to complex span tasks and vice versa (Soveri, Antfolk, Karlsson, Salo, & Laine, 2017; von Bastian & Oberauer, 2013).

To account for the transfer effect in WM training, similarity-based theories have proposed that the similarity between trained and untrained tasks is critical for successfully transferring training. For example, the specific process hypothesis suggested that training transfer required similar cognitive processes/components across tasks (Holmes, Gathercole, & Dunning, 2009; Dahlin, Neely, Larsson, Backman, & Nyberg, 2008). Similarly, according to the neural plasticity hypothesis proposed by Klingberg and colleagues, increased overlap in neural activity between trained and untrained tasks led to larger transfer effects (Klingberg, 2010). Although both theories have received support from subsequent studies (Constantinidis & Klingberg, 2016; Minear et al., 2016), they have also been challenged by some null findings. For example, it has been shown that WM training does not transfer well to reasoning tests or decision-making tasks, which are closely related to WM and involve the pFC (Kassai et al., 2019; Redick, 2019; Soveri, Karlsson, Waris, Grönholm-Nyman, & Laine, 2017).

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To address this issue, it is important to investigate the factors that determine the similarities between the trained and transfer tasks. Previous studies have suggested that both the stimulus type and the task structure could influence the similarity between different VWM tasks. In terms of stimuli type, Spelke and Kinzler (2007) have suggested that human visual cognition includes several evolutionary critical, domain-specific core knowledge systems (such as objects, agents, actions, numbers, and locations), and different domains are supported by dissociated cognitive and neural substrates. This hypothesis was supported in recent VWM studies. For example, some studies have revealed distinct ventral and dorsal neural pathways for object and spatial WM (Postle, Stern, Rosen, & Corkin, 2000). A series of following behavioral and neural imaging studies revealed that VWM for objects, locations, and actions exhibited independent memory capacity (Shen, Gao, Ding, Zhou, & Huang, 2014; Wood, 2007, 2008), showed no dual-task interference (Ding et al., 2015; Wood, 2011), and recruited dissociated neural substrates (Cai et al., 2018). As a result, it has been found that WM training transferring between stimuli types within the same domain (e.g., from color to orientation or shape, all belong to the nonspatial visual domain) is easier than across different domains (e.g., from color to digit, color belongs to visual domain whereas digit belongs to the verbal domain; Norris, Hall, & Gathercole, 2019; Buschkuhl, Jaeggi, Mueller, Shah, & Jonides, 2017; Gaspar, Neider, Simons, McCarley, & Kramer, 2013).

In terms of task structure, it has been suggested that changes in local elements (“subroutines”) do not affect transfer, whereas changes in the overall task framework can impair transfer (Gathercole, Dunning, Holmes, & Norris, 2019; Taatgen, 2013). Recent studies have supported this hypothesis by demonstrating that changes in stimulus modality (visual or auditory) or retrieval responses (change detection or delay estimation) did not limit training transfer (Wang & Qian, 2020; Norris et al., 2019). In contrast, changes from an n -back task to a complex span task may affect information flow and the transfer effect (Soveri, Antfolk, et al., 2017; Au et al., 2015). In this case, the information flow in the n -back task included encoding, comparison, and updating, whereas the complex span task included encoding, switching, and retrieval.

However, several questions remain unanswered. First, although successful transfer has been observed for within-domain changes in stimuli type (e.g., from color to orientation) or changes in the local elements of the task structure (e.g., from recall to change detection; Wang & Qian, 2020; Norris et al., 2019), it remains an important open question whether the combined changes in stimulus type and task structure could affect the transfer effect. Second, the cognitive components that change because of training have not yet been identified. The effects of WM training are usually estimated based on the response accuracy, which reflects the combined outcomes of WM

capacity and precision (Pergher, Wittevrongel, Tournoy, Schoenmakers, & Van Hulle, 2018; Xu, Adam, Fang, & Vogel, 2018). These effects might be separated better if model-fitting approaches are used in conjunction with an appropriate control group and control conditions. Third, it is important to directly test the neural similarity hypothesis by examining whether the training and transfer tasks share common neural substrates and how training could change the neural responses in both tasks. Here, the shared neural substrates refer to the common neural indices that track WM performances both at the group level (i.e., the memory load effect) and at the individual level.

To address these issues, we trained participants on a color delay estimation task for 12 consecutive 1-hr sessions and examined the training effect and training transfers to other tasks, such as the color perception task, orientation change detection task, spatial 2-back task, symmetry span task, and Raven reasoning test 1 day and 3 months after training. A mixed model was used to separately estimate the color WM capacity and precision before and after training (Zhang & Luck, 2008), which allowed us to identify the cognitive components underlying the training effect. In addition, we recorded the EEG responses in the trained color delay estimation task and the orientation change detection task, allowing us to investigate the neural mechanisms underlying the training and transfer effects. We compared the neural signatures underlying the capacity of these two VWM tasks, which could be used to directly test the neural similarity hypothesis for the transfer effect. We focused on the parietal-occipital negative slow wave and alpha suppression, which has been found to predict WM capacities in a similar task (Fukuda, Mance, & Vogel, 2015). Additionally, we did exploratory analyses in a broader frequency range (theta, 4–7 Hz; alpha, 8–13 Hz; and beta, 14–30 Hz) to see if we could find shared neural indices for the training and transfer tasks. According to the neural similarity hypothesis, we would predict a significant behavioral transfer effect if the two tasks share common neural substrates.

METHODS

Participants

Forty-nine participants were randomly assigned to two groups: the training group (25 participants, female = 16, age = 20.40 ± 2.24) or the control group (24 participants, female = 14, age = 22.80 ± 2.72). All participants completed the pretraining and first posttraining tests; however, three participants in the training group and two participants in the control group dropped out before the second posttraining test 3 months later. The number of participants was chosen based on previous training studies (Jordan et al., 2020; Norris et al., 2019) and related EEG studies (Fukuda et al., 2015; Vogel & Machizawa, 2004). All participants had normal or corrected-to-normal

vision and no history of neurological or psychiatric problems. Informed written consent was obtained from all participants before the experiment. The behavioral and EEG studies were approved by the institutional review board of the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University.

Materials and Procedures

All participants participated in a pretraining test (“Pre”), 12-day color WM training (with different difficulty levels for the training and control groups, see below), and two posttraining tests. The first posttraining test (“Post1”) was carried out the day after training, and the second posttraining test (“Post2”) was carried out 3 months after training. In each test, participants completed a series of cognitive tasks to test the training and transfer effects.

Training Task and Procedure

The color delay estimation training task was adapted from a previous study (Zhang & Luck, 2008). In the delay estimation task, several colored squares were presented on a gray background at a distance of 60cm from the participant. Each colored square in the sample array had a visual angle of $2 \times 2^\circ$ and was centered on an invisible circle with a radius of 4.5° . The positions of the colored squares were chosen at random from a set of eight locations spaced equally around the circle. The color recall wheel was 2.2° thick, had a radius of 8.2° , and was centered on the monitor. The color recall wheel included 180 color values that were distributed evenly around a circle in the CIE L*a*b* space, with the center at $L = 70$, $a = 20$, and $b = 38$ and a

radius of 60. The colors in the sample array were randomly selected from these colors without replication in each trial, with a minimum difference of 15° between colors. In each trial, a 100-msec sample array was shown, followed by a 900-msec delay period with a central fixation cross and a probe display with a maximum RT of 8 sec. The probe display included a recall wheel and several black outlined squares in the area where the sample array had been located, with one square thicker to indicate the item to be recalled. The participants were instructed to choose the color of the target item from the recall wheel as precisely as possible by moving the mouse and clicking the color in the wheel. When the participants moved the mouse, a color square appeared in the center of the screen, which was updated in real time and matched the color on the wheel closest to the cursor. We presented the color wheel with a random rotation in different trials to reduce potential influences from spatial memory or action plans. After the participant responded, feedback was presented for 250 msec to indicate the error distance (in degrees) between the correct color and the chosen color (Figure 1A).

The task paradigms in the training and control groups were identical except for the task difficulty, that is, only Set Size 1 (SS1) was used. Compared with non-WM tasks, the low-load, nonadaptive color WM task in the control group could better control the task-related factors, such as task structure, visual perception, and motor response. Such a control group is widely used in previous training studies (Dunning & Holmes, 2014; Holmes et al., 2009). In the training group, the task began with three color squares that were adaptively adjusted using the two-up/two-down procedure; that is, if the participants chose

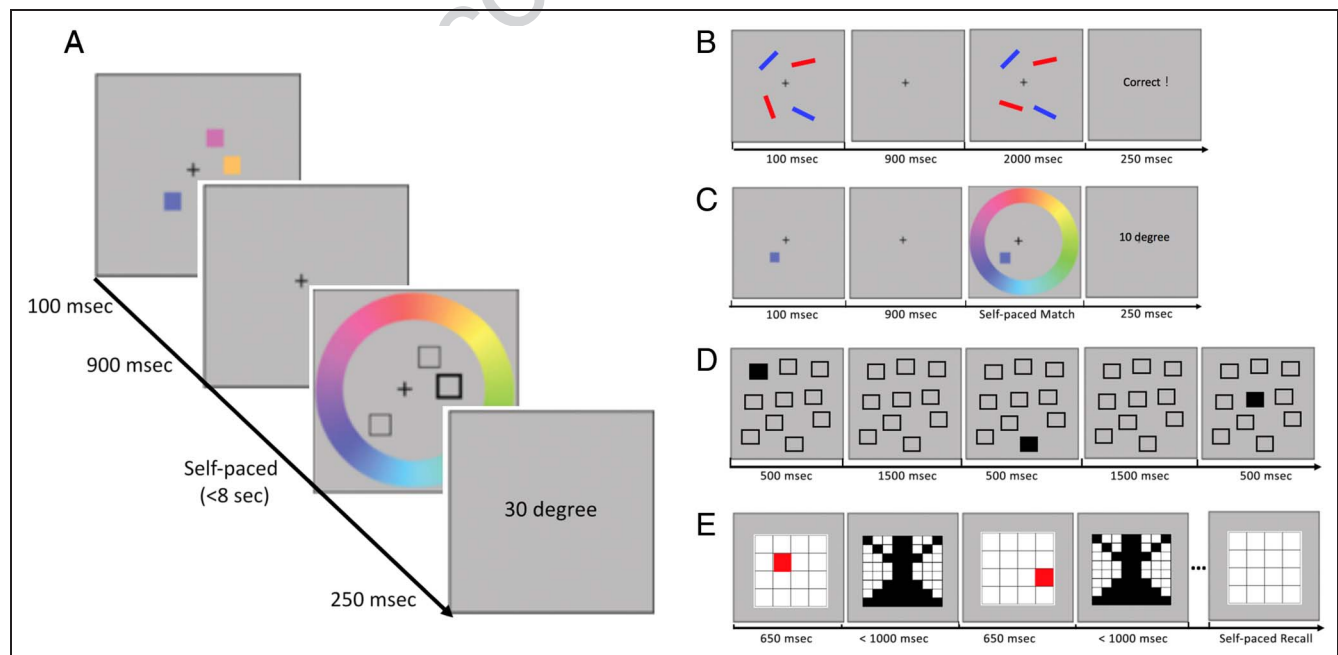


Figure 1. Experimental procedures. (A) Color delay estimation task. (B) Orientation change detection task. (C) Color perception task. (D) Spatial 2-back task. (E) Symmetry span task.

the correct response in two consecutive trials (i.e., the errors were less than 18°; this criterion was empirically chosen based on the mean recall errors in the pretest color WM task across participants), the number of color squares increased by one (with a maximum of eight squares). In contrast, if the participants chose incorrect response in two consecutive trials (i.e., the errors were larger than 18°), the number of squares decreased by one (with a minimum of three squares). In the control group, only one color square was used, and participants were required to recall the color as precisely as possible. Participants in both groups participated in 12 consecutive training sessions. Each session included 900 trials and lasted 1–1.5 hr. The participants were given a short break every 100 trials.

Pre- and Posttraining Tests

The same tasks were used in the Pre, Post1, and Post2 tests and are described below (Figure 1). EEG responses were recorded during the color delay estimation task and the orientation change detection task.

Color Delay Estimation Task

An independent color delay estimation task was used to examine the training effect. The task was the same as the training task, except that the number of colored squares in the sample array was one, two, three, four, six, or eight (Figure 1A). There were 80 trials for each set size, and the 480 trials were randomly divided across three runs. The participants rested for 3 min between runs. Before the formal experiment, the participants were presented with 12 practice trials to ensure that they were familiar with the procedure.

Orientation Change Detection Task

An orientation change detection task with distractions was used to evaluate the transfer effect (Li et al., 2017; Figure 1B). In each trial, several red- and blue-oriented bars were displayed near the center of the screen for 100 msec. The participants were instructed to remember the orientations of the red bars (“targets”), whereas they were told to ignore the orientations of the blues bars (“distractors”). All stimulus arrays were presented on a gray background in one of two $4^\circ \times 7.3^\circ$ rectangular regions that were centered 3° to the left or right of a central fixation cross. The position of the stimulus was randomized for each trial, with the constraint that the distance between items was at least 2° (center to center). After a blank interval of 900 msec, a test array was presented, and participants were asked to determine whether the orientations of the red bars had changed. The participants responded by pressing the corresponding button on an RT box with their left or right index finger, with an RT limit of 2 sec. The yes/no response buttons were counterbalanced across participants. In half of the trials, one of the red bars was

rotated by 45° . This task had six conditions: including two, four, six, or eight red bars, as well as two red bars plus two blue bars and four red bars plus two blue bars (labeled as “T2,” “T4,” “T6,” “T8,” “T2D2,” and “T4D2,” respectively, where “T” indicates targets and “D” indicates distractors). There were 90 trials for each condition, which were randomly mixed and equally divided into three runs. The participants rested for 3 min between runs. Before the formal experiment, 12 practice trials were completed.

Color Perception Task

A color perception task was used to evaluate whether the color WM training improved primary color perception. The task procedure was similar to that of the delay estimation task, except that only one colored square was presented during both the encoding and probe periods, and participants needed to match its color from the color wheel as precisely as possible only during the probe period (Figure 1C). There were 12 practice trials and 100 formal trials. The color perception precision was measured as the reciprocal of the mean raw error distance (in degrees), which was calculated by subtracting the angle of the correct color from the angle of the chosen color (Bays & Husain, 2008).

Spatial 2-Back Task

To evaluate whether color WM training could transfer to other WM tasks with different cognitive routines, we included a spatial 2-back task. In this task, 10 fixed squares with black outlines were always displayed on the screen. In each trial, one of these squares flashed for 500 msec, with a 1.5-sec interval between trials (Figure 1D). Participants were instructed to determine whether the location of the current square was the same as that of the previous square by pressing “F” or “K” on the keyboard. The response had to be made before the next trial began (within 2 sec). This task included 96 trials across four runs, with participants taking a 1-min break between runs. The participants started the formal experiment when their task accuracy in the practice sessions exceeded 70%. The task performance index was d' , which was calculated with the following formula: $d' = z(\text{hit}) - z(\text{fa})$, where the hit rate (“hit”) indicates the proportion of successfully detected changes in the targets and the false alarm rate (“fa”) indicates the proportion of incorrectly reported changes in the targets. Both the hit and false alarm rates were transformed into z scores before subtraction.

Symmetry Span Task

We investigated whether color WM training could be transferred to a complex spatial span task; this task paradigm was adapted from a previous study (Unsworth, Heitz, Schrock, & Engle, 2005; Kane et al., 2004). In each trial, an array of different spatial locations was sequentially presented as a

red square on a 4×4 checkerboard, with a symmetry judgment task between presentations (Figure 1E). Each spatial location was shown for 650 msec, and the participants were required to remember these locations. In the symmetry judgment task, the participants were instructed to determine whether a figure with 8×8 black–white squares was axially symmetrical by clicking the “True” or “False” icons on the screen within 1 sec. After all the spatial locations were presented, the participants were required to recall all the locations in the order they were presented by clicking the squares on the checkboard with the mouse. There was no time limit for the recall stage. The task began with two locations and was adaptively adjusted using the two-up/two-down procedure; that is, if the participants recalled all the locations correctly in two consecutive trials, the number of locations increased by one (with a maximum of eight locations). If the participants made two errors in a row, the number of locations decreased by one (with a minimum of two locations). The task included 12 trials. Before the task, participants were presented with three practice trials to ensure that they were familiar with the experimental procedure. In this task, the memory span was measured by the total number of items within trials in which all items were correctly recalled.

Raven’s Advanced Progressive Matrices

The Raven’s advanced progressive matrices (RAPM) test (Hamel & Schmittmann, 2006) was used to assess whether WM training could transfer to general intelligence. All 36 questions were divided into odd and even sets for use in the pretraining and first posttraining tests. The questions used in the two tests were counterbalanced across participants. In each test, participants had 10 min to complete all the questions. The performance in the RAPM test was evaluated based on the total number of correctly answered questions.

EEG Data Collection

EEG responses for the color delay estimation task and the orientation change detection task were recorded during all three tests using a 64-channel Biosemi ActiveTwo EEG system (Biosemi, Inc.). During the EEG recordings, participants sat 60 cm away from the computer screen in a soundproof room with adjustable light levels. The sampling rate was set to 1024 Hz, the Ag–AgCl electrodes were mounted according to the 10–20 system, and the impedances of all the electrodes were kept below 5 k Ω .

Behavioral Data Analysis

Estimation of the Capacity and Precision in the Color Delay Estimation Task

We examined the overall training effect in the color delay estimation task by comparing the individual memory

capacity and precision indices before and after training. To determine the individual memory capacity and precision for the color task, we first estimated the response probability of the targets (pT) and the memory precision (K) in each set size with a mixed model via an open-source toolbox (Schneegans & Bays, 2016; <https://bayslab.com/toolbox/>). To achieve stable estimations in high memory load conditions, we combined the SS6 and SS8 trials (“SS68” indicates the combined high memory load condition). The memory capacity was calculated separately for each set size by multiplying the pT value by the set size (Wang, Itthipuripat, & Ku, 2019). Then, we averaged the capacities only when they reached a plateau for evaluating individual color WM capacity (Fukuda et al., 2015; Vogel & Machizawa, 2004). In the current study, paired t tests in the pretraining test revealed that capacities increased from SS1 to SS3 ($ps < .002$) and then plateaued ($ps > .489$); thus, we averaged capacities of SS4 and higher memory load trials as the individual WM capacity. In addition, we used the precision of the SS1 trial as the memory precision index. This index was chosen because the memory capacity in SS1 was nearly 1 (larger than 0.980 in Pre, Post1, and Post2). Thus, it could minimize the trade-off between capacity and precision (Wang, Itthipuripat, & Ku, 2020; Roggeman, Klingberg, Feenstra, Compte, & Almeida, 2014). To examine the immediate training effect, we used a two-way mixed ANOVA for each index, with the test (Pre and Post1) as a within-subject variable and the group (training and control) as a between-subject variable. If the interaction effect was found to be significant, post hoc paired t tests were performed. A similar analysis was used to investigate the long-term training effect (Pre and Post2). As a few participants did not finish the Post2 test, different number of participants were included when examining the immediate training effect and long-term training effect to maximize the statistical power.

Estimation of the Capacity in the Orientation Change Detection Task

To estimate the WM orientation capacity, we only included trials without distractors (T2, T4, T6, and T8), which better matched the color WM tasks in the binding process (color–location vs. orientation–location) and the involvement of filtering process. We calculated Cowan’s K in each condition with the following formula: $K = \text{set size} \times (\text{hit rate} - \text{false alarm rate})$; (Cowan, 2001), where the hit rate refers to the successful detection of target changes and the false alarm rate refers to incorrect reports of target changes. We averaged the K values of the T4, T6, and T8 trials as an index for individual orientation WM capacity. This index was chosen because paired t tests for the pretraining test revealed that the K values increased from T2 to T4 ($ps < .003$) and then plateaued ($ps > .087$). Similar two-way mixed ANOVA and post hoc tests were used to evaluate the transfer effects. Additionally, Pearson correlations between the color and orientation capacities were

carried out in each test to assess whether there were task-specific WM capacities.

Estimation of the Attention Control Ability

The attention control index (“AttIdx”) in the orientation change detection task was estimated with the following formula: $\text{AttIdx} = 2 + K(\text{T4D2}) - K(\text{T4})$ (Li et al., 2017), where T4D2 refers to the condition with four targets and two distractors. The AttIdx reflects the ability of an individual to ignore/suppress task-irrelevant distractors, with a higher AttIdx score indicating better attention control ability. To evaluate the far transfer effect in other cognitive processes, the attention control index and the behavioral indices of the color perception task, 2-back task, complex span task, and RAPM were analyzed with similar ANOVAs and post hoc tests.

EEG Data Preprocessing

EEG data preprocessing was conducted in EEGLAB (Delorme & Makeig, 2004; www.sccn.ucsd.edu/eeglab/) and with customized MATLAB scripts (The Mathworks, Inc.). EEG data were downsampled to 256 Hz, processed with a bandpass filter of 0.1–30 Hz, and segmented into epochs of –1 to 2 sec relative to the stimulus onset. After segmentation, we interpolated poor channels (e.g., those with large drifts and/or lost signals) using the “spherical” method in EEGLAB, referenced the data to the median of all electrodes, and removed the baseline by subtracting the averaged activities within the prestimulus interval (–200 to 0 msec). Furthermore, we identified and removed horizontal and vertical eye movements using an independent component analysis algorithm (runica function in EEGLAB). Finally, the preprocessed data were verified with a careful visual inspection.

Parieto-occipital Negative Slow Wave and Alpha Power Suppression

We tested whether the delay period parieto-occipital negative slow wave and alpha power suppression were correlated with individual WM capacity for colors or orientations (Fukuda et al., 2015). Following a previous study, the delay period was defined as 300–900 msec after stimulus onset (i.e., 200 msec after the delay onset and 100 msec before the probe period), and the parieto-occipital electrodes included P1–P10, PO3, PO4, PO7, PO8, O1, O2, Pz, POz, Oz, and Lz (based on the 10–20 EEG system). First, paired *t* tests between adjacent set sizes conditions were performed to identify the turning points of memory capacity. Then, we subtracted the mean neural activities of the subcapacity set sizes from the mean measures in the supracapacity condition. Pearson correlations were used to determine whether these neural signals reflected WM capacity for colors or orientations, and independent *t* tests

were used to evaluate whether training effects differed between groups.

Exploratory Analysis of the Power Strength Associated with WM Capacity

We also investigated whether the power strengths in other brain regions or other frequencies were correlated with individual WM capacity for colors or orientations. The present study mainly focused on theta (4–7 Hz), alpha (8–13 Hz), and beta (14–30 Hz) power because previous studies have linked these neural oscillations to the maintenance of VWM (Bahramisharif, Jensen, Jacobs, & Lisman, 2018; Roux & Uhlhaas, 2014). To extract the power strength during each task, time–frequency decomposition was performed on the preprocessed data using the doth-wave function (Samaha, Sprague, & Postle, 2016; <https://samahalab.ucsc.edu/resources>). Specifically, the preprocessed data were convolved with a family of wavelets ranging from 4 to 30 Hz in 1-Hz steps, and the wavelet cycles were set to increase linearly as a function of the frequency between the third and eighth cycles. The power strength was extracted from the resulting complex time series by squaring the absolute value of the time series (μV^2), averaged across each frequency band, and normalized by dividing the average power by that of the prestimulus baseline period (–400 to 0 msec).

To explore which power strengths were associated with individuals’ WM capacity, we focused on data from the pre-training test to prevent any influence from training (such as changes in task strategies) and included participants in both groups (there were no differences between the groups before training). A three-step procedure was used. First, we identified the electrodes where the delay period power strengths tracked the WM capacity at the group level, that is, increased with memory loads and reached a plateau in higher memory loads. To accomplish this, repeated-measures ANOVA and paired-sample *t* tests were performed across set sizes to determine all the candidate electrodes across the whole brain; then, a Monte Carlo nonparametric test was used to identify significant electrode clusters (Maris & Oostenveld, 2007). Specifically, we shuffled the power strength 2500 times in each set size to generate a set of electrode clusters that followed the behavioral performance (“shuffled clusters”). Real electrode clusters that were 95% larger than the shuffled clusters were identified as brain areas of interest. Second, within these brain areas, we narrowed down the time windows when the power strengths continuously/stably tracked the WM capacity at the group level (Fukuda et al., 2015). Similar ANOVA and *t* tests procedures were used to obtain all the time points during the delay period that could track the WM capacity at the group level, and a Monte Carlo test was used to identify significant time clusters with lengths longer than 95% of the shuffled clusters. Third, Pearson correlation analyses across participants were used to determine whether the power strengths

could predict individuals' WM capacity for the color or orientation tasks. We performed a separate power analysis for each frequency band, and the power strengths that reflected the WM capacity at the group level were tested further to determine whether they predicted the WM capacity at the individual level. Only the power strengths that predicted the WM capacity at both the group and individual levels were identified as neural indices of the WM task. This procedure was performed separately for each task. Finally, we investigated how training affected these neural indices.

RESULTS

Behavioral Results

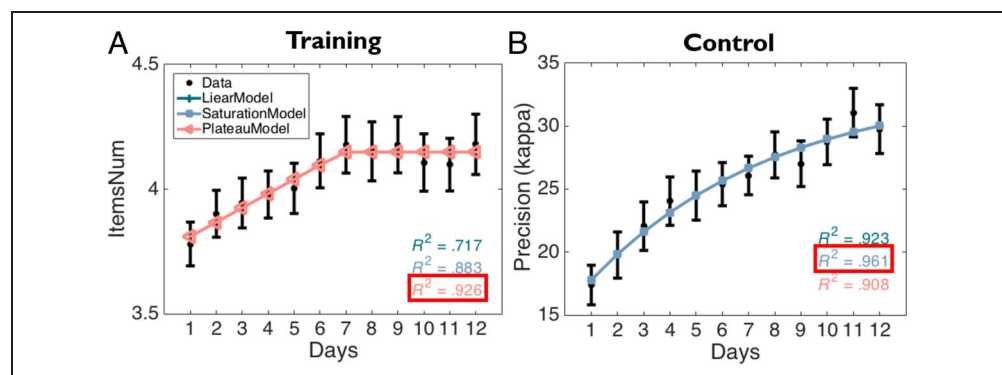
Behavioral Performance during Training

In the adaptive training group, the mean number of items increased gradually from first to seventh day and thereafter reached a plateau (plateau model fit best: $R^2 = .926$; linear model: $R^2 = .727$; saturation model: $R^2 = .883$). In the nonadaptive control group, the memory precision was estimated from the mixture model, which gradually improved across training (the saturation model fit best: $R^2 = .961$; linear model: $R^2 = .923$; saturation model: $R^2 = .908$; Figure 2B). These results confirmed the efficiency of training.

Overall Behavioral Performance before and after Training

The overall task performance of the participants is summarized in Table 1. Participants with poor behavioral performance (greater than 2.5 SDs from the group mean) in the pre- or posttraining tests were separately excluded from each task. In addition, data from four participants in the Post1 test for the symmetry span task were lost because of technical difficulties, and three participants in the color perception task were excluded because of a self-reported nonvisual strategy in the pretraining test. Two-sample t tests revealed that the training and control groups had comparable pretraining performance baselines in all tasks ($ps > .158$, $BF_{s10} < 0.430$).

Figure 2. Behavioral performance during the training in the training group and the control group. The model fittings procedures were adapted from a previous study (Bays, 2018).



Training Improved the WM Capacity for Colors but Not Orientations

For the color WM capacity, a two-way mixed ANOVA revealed a significant interaction effect between the test (Pre/Post1) and group (training/control), $F(1, 44) = 7.236$, $p = .010$, $BF_{10} = 13.347$. A post hoc paired t test revealed that training significantly increased the WM capacity in the training group, $t(22) = 5.586$, $p < .001$, $BF_{10} = 1727.318$, whereas no significant change was observed in the control group, $t(22) = 1.356$, $p = .189$, $BF_{10} = 0.490$. Moreover, this training effect was sustained 3 months later. There was a significant interaction effect between the test (Pre/Post2) and group, $F(1, 39) = 4.415$, $p = .049$, $BF_{10} = 2.724$, indicating that the performance of the training group improved significantly, $t(19) = 2.844$, $p = .010$, $BF_{10} = 4.966$, whereas the performance of the control group did not, $t(20) = 1.108$, $p = .281$, $BF_{10} = 0.391$ (Figure 3A). To test the training effect in color WM task in each set size separately, two-way mixed ANOVAs revealed only the capacity improvements in higher memory loads were significant in posttraining tests (interaction effects between test and group in SS68: $ps < .034$, $BF_{s10} > 2.549$; other set sizes: $ps > .493$, $BF_{s10} < 0.333$).

For the orientation task, there was a main effect of test, $F(1, 41) = 5.029$, $p = .030$, $BF_{10} = 1.467$, but there was no main effect of group, $F(1, 41) = 0.300$, $p = .573$, $BF_{10} = 0.427$, or Group \times Test interaction, $F(1, 41) = 1.164$, $p = .287$, $BF_{10} = 0.417$. Further simple effect analysis revealed no increase in the control group, $t(20) = 0.958$, $p = .349$, $BF_{10} = 0.342$, and only a small although significant increase in the training group, $t(21) = 2.112$, $p = .047$, $BF_{10} = 1.414$. In the Post2 test, no significant main effects or interaction effects were observed ($ps > .244$, $BF_{s10} < 0.317$; Figure 3B). Similarly, there were no transfers on orientation WM capacity in any set size in two posttraining conditions (interaction effect between groups and tests: $ps > .170$, $BF_{s10} < 0.734$). These results did not support for a transfer effect in the orientation task.

No Correlation between WM Capacities for Colors and Orientations

In addition to the lack of transfer effect, the Pearson correlation analyses revealed no significant correlations

Table 1. Summary of the Behavioral Results

<i>Task</i>	<i>Index</i>	<i>Training Group</i>						<i>Control Group</i>					
		<i>Pre</i>		<i>Post1</i>		<i>Post2</i>		<i>Pre</i>		<i>Post1</i>		<i>Post2</i>	
		<i>n</i>	<i>Mean (SD)</i>	<i>n</i>	<i>Mean (SD)</i>	<i>n</i>	<i>Mean (SD)</i>	<i>n</i>	<i>Mean (SD)</i>	<i>n</i>	<i>Mean (SD)</i>	<i>n</i>	<i>Mean (SD)</i>
Color WM	Capacity	23	2.31 (0.59)	23	3.08 (0.63)	20	2.84 (0.64)	23	2.27 (0.53)	23	2.47 (0.72)	21	2.45 (0.57)
	Precision	23	17.02 (6.45)	23	20.69 (7.24)	20	19.81 (8.43)	23	17.39 (7.17)	23	28.95 (10.08)	21	23.80 (10.11)
Orientation WM	Cowan's <i>K</i>	22	1.97 (0.97)	22	2.30 (0.91)	18	1.99 (0.70)	21	1.93 (0.88)	21	2.05 (0.77)	19	1.84 (0.62)
	AttIdx	22	1.74 (0.69)	22	1.86 (0.37)	18	1.72 (0.46)	21	1.91 (0.48)	21	1.59 (0.37)	19	1.72 (0.59)
Color perception	deg ⁻¹	19	0.16 (0.04)	19	0.17 (0.04)	16	0.17 (0.06)	21	0.19 (0.06)	21	0.25 (0.07)	19	0.24 (0.07)
2-back	<i>d'</i>	23	2.61 (1.10)	23	3.28 (0.65)	20	2.95 (0.83)	22	2.47 (1.05)	22	3.19 (0.68)	20	3.09 (0.94)
Symmetry span	Total score	18	23.72 (10.13)	18	27.89 (4.59)	15	28.13 (8.72)	22	24.18 (9.67)	22	27.50 (6.71)	20	29.35 (7.81)
RAPM	Corrected items	24	12.17 (1.83)	24	12.71 (2.23)	–	–	23	12.04 (1.82)	23	13.13 (2.96)	–	–

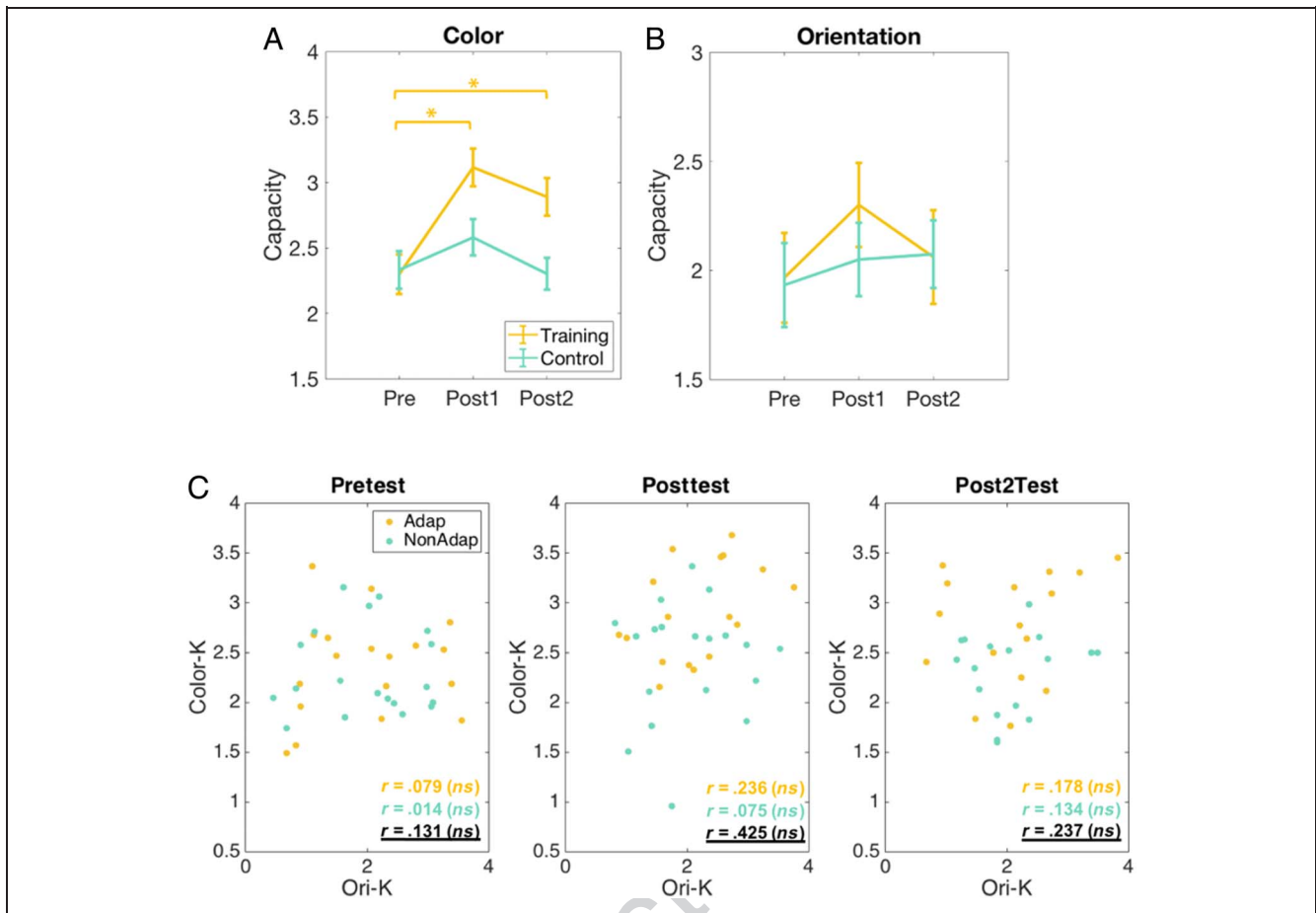


Figure 3. (A, B). Training reliably improved the WM capacity for colors but not orientations. (C) No correlations between WM capacity for colors and orientations were observed in the Pre, Post1, and Post2 tests. The yellow and green dots indicate participants in the training group and control group, respectively. The R values are the correlation coefficients between the WM capacities for colors and orientations among participants in the training group (yellow), the control group (green), and both groups (black).

between the WM capacities for colors and orientations in any of the three tests, regardless of whether each group was analyzed separately or combined ($ps > .320$, $BF_{10} < 0.443$, expect relatively weaker BF evidence in Post1 training group, $p = .166$, $BF_{10} = 1.142$, and relatively weak p evidence in Post1 combined participants, $p = .089$, $BF_{10} = 0.532$; Figure 3C). These results suggest that the color recall task and orientation change detection task involve distinct cognitive processes and different aspects of WM capacity.

Training Did Not Improve the WM Precision or Perception for Colors

In terms of WM precision for color, two-way mixed ANOVA revealed a significant interaction effect between the test (Pre/Post1) and group (training/control), $F(1, 44) = 8.954$, $p = .005$, $BF_{10} = 26.826$. Post hoc paired t tests showed that the recall precision increased after training in both groups ($ps < .043$, $BF_{10} > 1.479$), with a larger effect observed in the control group (independent t test on change degree), $t(44) = 2.992$, $p = .005$, $BF_{10} =$

9.122. Although the test main effect was still significant 3 months later, $F(1, 39) = 9.094$, $p = .004$, $BF_{10} = 7.897$, the difference between the groups was not maintained, as indicated by the nonsignificant interaction effect between the test (Pre vs. Post2) and group, $F(1, 39) = 1.714$, $p = .198$, $BF_{10} = 0.722$. Two-way mixed ANOVAs revealed no differences in precision in other set sizes after training ($ps > .198$, $BF_{10} < 0.677$). These results suggest that the test–retest procedure generally improved the WM precision in both groups, with nonadaptive low-capacity training showing a larger improvement over time.

We found an improvement in the accuracy of color perception in the control group, which was consistent with the training effect of WM precision observed in this group. In particular, two-way mixed ANOVA revealed a significant interaction effect between the test (Pre/Post1) and group (training/control), $F(1, 38) = 7.279$, $p = .010$, $BF_{10} = 15.765$, indicating a significant increase in the control group, $t(20) = 4.866$, $p < .001$, $BF_{10} = 293.041$, but not in the training group, $t(18) = 1.097$, $p = .287$, $BF_{10} = 0.402$. Moreover, this improvement in color perception was maintained in the Post2 test: interaction effect, $F(1,$

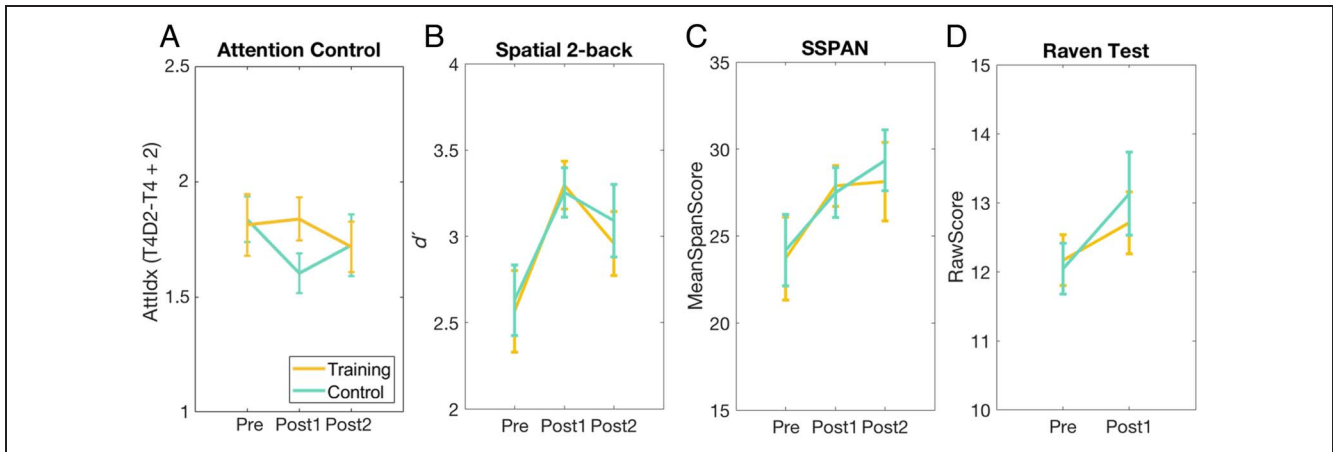


Figure 4. Training did not improve the performance in the attention control test, spatial 2-back task, symmetry span task, or Raven reasoning task.

33) = 4.512, $p = .041$, $BF_{10} = 2.695$; control group, $t(18) = 2.712$, $p = .014$, $BF_{10} = 3.913$; training group, $t(15) = 0.247$, $p = .808$, $BF_{10} = 0.262$.

Training Did Not Transfer to Other Cognitive Tasks

In terms of attention control ability, there was a marginally significant interaction effect between the test (Pre/Post1) and group (training/control), $F(1, 41) = 3.822$, $p = .057$, $BF_{10} = 0.537$. A post hoc paired t test revealed that the

attention control ability remained unchanged in the training group, $t(21) = 0.697$, $p = .493$, $BF_{10} = 0.278$, but worsened in the control group, $t(20) = 2.191$, $p = .040$, $BF_{10} = 1.612$. No such differences were observed in the second posttraining test ($ps > .459$, $BF_{10} < 0.306$; Figure 4A).

For the spatial 2-back task, symmetry span task, and Raven reasoning task, there was a significant main effect of test ($ps < .031$, $BF_{10} \geq 1.378$) but no main or interaction effect of group ($ps > .461$, $BF_{10} < 0.320$; Figure 4B–D). Taken together, these findings suggest that the

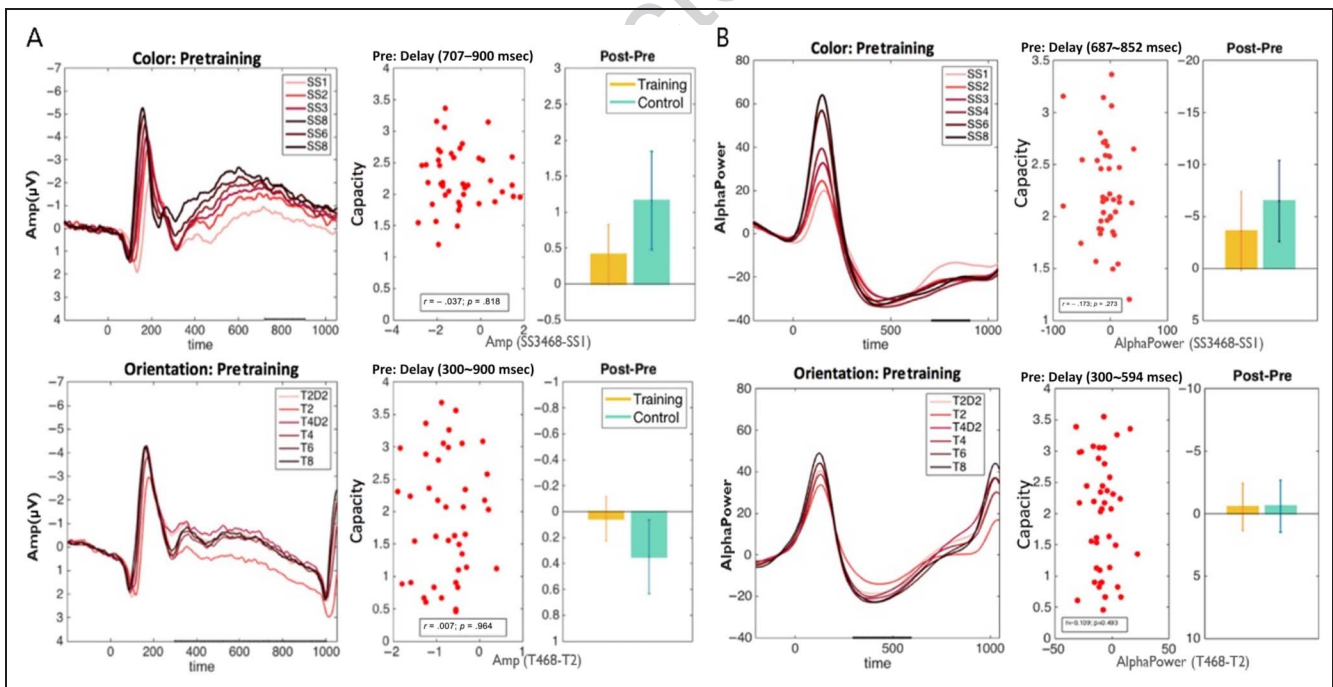


Figure 5. The results of parietal-occipital negative slow wave and parietal-occipital alpha power. (A) The parietal-occipital negative slow wave in the color delay estimation task and orientation change detection task, which reached plateaus at high memory load conditions (left). The signal increases between high and low memory loads during the delay period did not predict WM capacities for colors or orientations across participants (middle). WM training did not change these neural signals in either task (right). (B) The parietal-occipital alpha power in the color delay estimation and orientation change detection tasks. During the delay period, alpha power reached plateaus at high memory load conditions (left), alpha suppression between high and low memory loads did not predict WM capacities (middle), and WM training did not change alpha suppressions (right). The black bars at the bottom of the left panels indicate the time windows showing significant load effects which survived Monte Carlo nonparametric test (Fukuda et al., 2015).

training effect of color WM capacity did not transfer to attention control, spatial WM, or general reasoning ability.

EEG Results

Participants with poor behavioral performance (beyond 2.5 SDs from the group mean), poor EEG signal quality (less than 40 trials in any condition), or abnormal neural indices (beyond 2.5 SDs from the group mean) in the pre- or posttraining tests were excluded from the EEG analyses. As a result, in the training group, 19, 19, and 16 participants were included in the color WM task in the Pre, Post1, and Post2 tests, respectively, whereas 21, 21, and 18 participants were included in the orientation WM task. In the control group, 21, 21, and 19 participants were included in the color WM task in each test, whereas 20, 20, and 18 participants were included in the orientation WM task.

Parietal-occipital Negative Slow Wave and Alpha Power Suppression Did Not Predict WM Capacities for Colors or Orientations

Our results revealed that both the parietal-occipital negative slow wave and alpha power suppression reflected the behavioral performance at the group level in the color and orientation tasks. In color task, SS1 < SS2 (p <

.052, $BF_{s_{10}} > 2.726$) and no differences thereafter (p > .101, $BF_{s_{10}} < 0.606$); in orientation task, T2 > T4 (p < .001, $BF_{s_{10}} > 73.862$) and no differences thereafter (p > .114, $BF_{s_{10}} < 0.550$; Figure 5A–B, left). However, neither of these two signals predicted the individual capacities for colors or orientations (p > 0.273, $BF_{s_{10}} < 0.344$) or reflected the improvement in color WM capacity after training (p > 0.364, $BF_{s_{10}} < 0.424$; Figure 5A–B, right). Thus, these results provide partial evidence for previous findings.

Parietal Theta Power Suppression Predicted Color WM Capacity

An exploratory analysis revealed that suppression of parietal theta power during the early delay period (CP1, CP2, CPz, P1, P2, Pz, and POz, 300–540 msec) specifically reflected the color WM capacity (Figure 6A). At the group level, paired t tests revealed that the parietal theta power decreased from SS1 to SS4 (p < .013, $BF_{10} > 3.118$; except SS2 vs. SS3: $p = .789$, $BF_{10} = 0.173$) but did not differ among higher memory loads (SS4 vs. SS6 vs. SS8, t < 0.621, p > .583, $BF_{s_{10}} < 0.200$). At the individual level, Pearson correlation analyses revealed that the theta power suppression between low and high memory load (SS12–SS468) was specifically correlated with individual color WM capacity, $r(41) = .353$, $p = .023$, $BF_{10} = 2.320$,

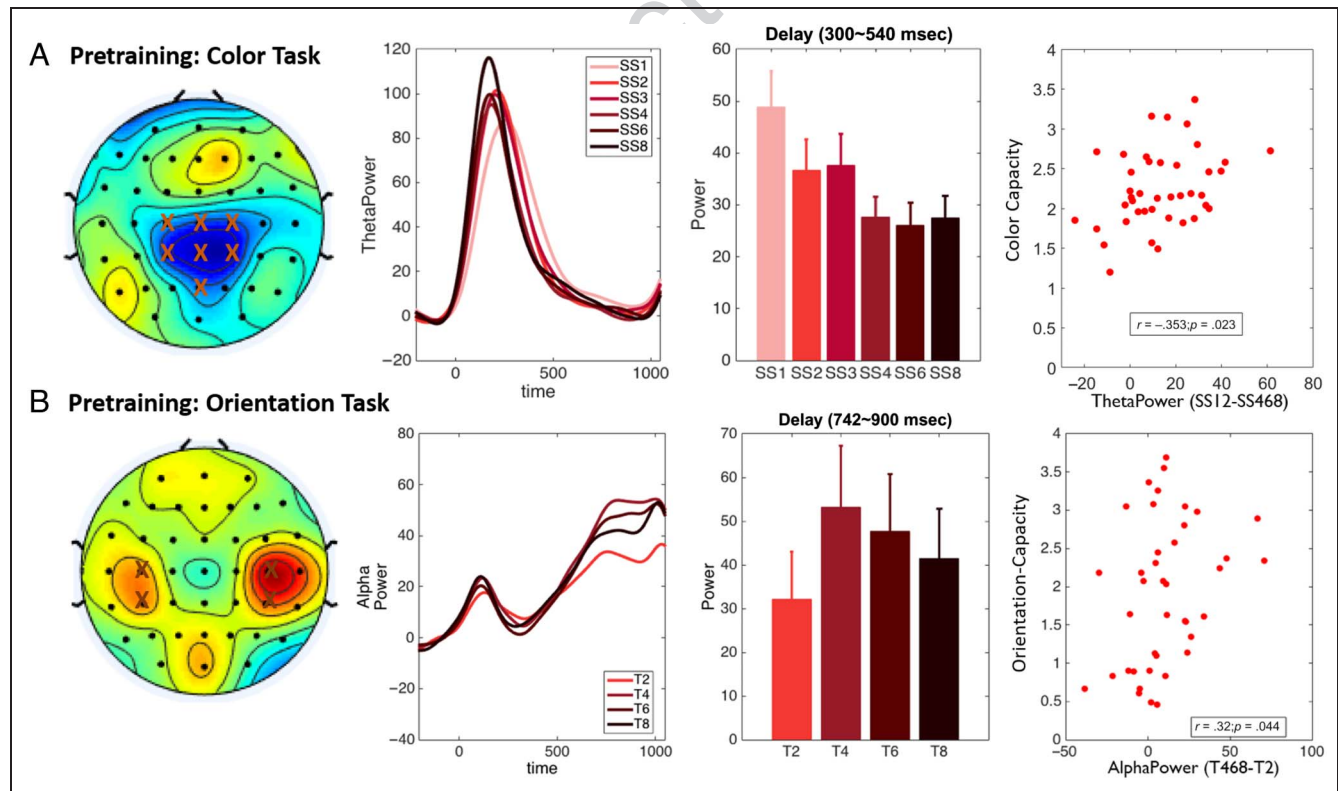


Figure 6. (A) In the color delay estimation task, parietal theta power suppression during the early delay period predicted the color WM capacity. (B) In the orientation change detection task, the temporoparietal alpha power increase during the late delay period predicted the orientation WM capacity. For the neural indices of WM capacities, the red crosses in the left panel indicate the specific electrodes of the signals, and the black bar at the bottom of the second panel indicates the specific time window.

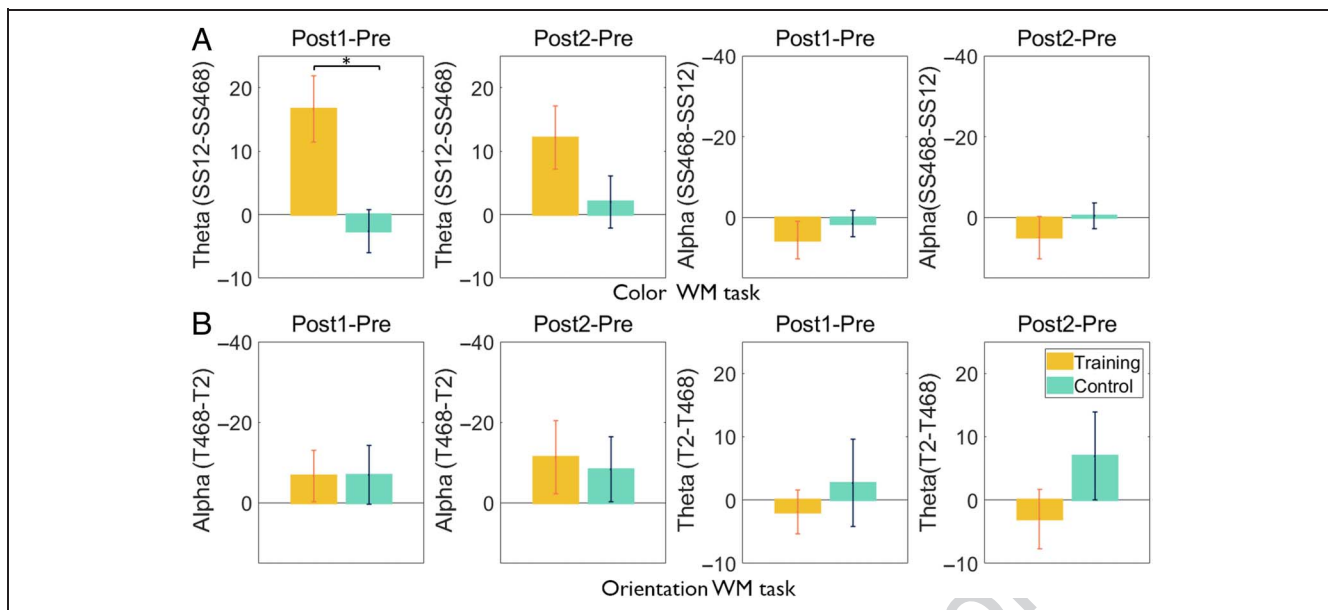


Figure 7. (A) In the color delay estimation task, training increased parietal theta suppression, which indexes WM capacity for colors (left); however, training did not increase the temporoparietal alpha power, which indexes WM capacity for orientations (right). (B) In the orientation change detection task, training did not change either neural index.

but not orientation WM capacity, $r(42) = .146, p = .356, BF_{10} = 0.290$.

Increase in Temporoparietal Alpha Power Predicted the Orientation WM Capacity

In the orientation WM task, the alpha power in the bilateral temporoparietal region during the late delay period (C3, CP3, C6, and CP6, 742–900 msec) predicted the orientation WM capacity (Figure 6B). At the group level, paired t tests revealed that the alpha power increased from T2 to T4, $t(41) = 3.406, p = .002, BF_{10} = 21.152$, but did not change further (T4 = T6 = T8, $p_s > .182, BF_{s10} < 0.391$). At the individual level, the change in alpha power (T468–T2) specifically predicted the orientation WM capacity across participants, $r(40) = .320, p = .044, BF_{10} = 1.932$, but did not predict the color WM capacity, $r(41) = .180, p = .260, BF_{10} = 0.359$. It should be noted that given the time window was very late in the delay, the identified alpha power might contain signals from the probe stage. Nevertheless, we believe this contamination is minimal. The set size effect in the probe stage for the change detection task should be similar to the delay period.

Training Increased Parietal Theta Power Suppression in the Color WM Task

Consistent with the increased color WM capacity after training and the positive correlation between parietal theta power suppression (SS12–SS468) and color WM capacity, independent t test revealed that the parietal theta

power during the color WM task decreased more (Post1 – Pre) in the training group than in the control group, $t(38) = 3.152, p = .003, BF_{10} = 12.257$; a similar trend (although statistically nonsignificant) was found 3 months later, $t(33) = 1.584, p = .123, BF_{10} = 0.850$ (Figure 7A, left). In contrast, training had no effect on the temporal–parietal alpha power increase in the color WM task in either group ($p_s > .244, BF_{s10} \leq 0.436$; Figure 7A, right). These results suggested that WM training specifically changed the neural index of color WM capacity.

Training Did Not Change Temporoparietal Alpha Power Increase in the Orientation WM Task

The temporoparietal alpha increase during the orientation WM task did not change after training in either group ($p_s > .229, BF_{s10} < 0.475$), confirming the limited training transfer effect on orientation WM capacity. In addition, training had no effect on parietal theta power suppression in the orientation WM task ($p_s > .587, BF_{s10} < 0.261$; Figure 7B).

DISCUSSION

The goal of the present study was to investigate the cognitive and neural mechanisms of VWM training, as well as its transfer effect. We found a significant and long-term training effect, which was consistent with previous studies (Sandberg & Stigsdotter Neely, 2016; Jaeggi, Buschkuhl, Jonides, & Shah, 2011). More importantly, we presented several important results that could contribute to our understanding of the training effect and its limited transfer

effect. First, our model-fitting results revealed that VWM training mainly improved WM capacity rather than recall precision, elucidating the specific cognitive component underlying the training effect. Second, our behavioral results revealed that color recall training cannot be transferred to an orientation recognition task, suggesting that the combined changes in the stimulus and task structure introduced additional transfer limits, lending support to similarity-based transfer theories. Third, we found that individuals' WM capacity for the color and orientation tasks did not correlate with one another, suggesting that the cognitive mechanisms are distinct. Finally, our EEG results indicated that WM training changed only task-specific neural activity, providing a neural explanation for training and the limited transfer effect.

The model-fitting results revealed that VWM training improved memory capacity rather than precision. These results were consistent with some recent studies, which have suggested that memory capacity and precision are supported by separate neural mechanisms. For example, recent fMRI studies discovered that sustained parietal activity was linked to WM capacity, whereas occipital neural representation fidelity was closely related to memory recall precision (Zhao, Kuai, Zanto, & Ku, 2020; Ku, Bodner, & Zhou, 2015). Follow-up noninvasive electrical stimulation studies confirmed these findings by showing that parietal stimulation changed memory capacity but not memory precision (Wang et al., 2019, 2020). Because the majority of previous studies on WM training used *n*-back or complex span tasks and thus could not separate the training effects of central executive processes from memory storage ability (Norris et al., 2019; Pergher et al., 2018), a recent training study focused on the training effect of the memory storage process and found that the training for the color change detection task reliably increased memory capacity for colors (Xu et al., 2018). However, this study did not discuss whether training improved WM precision. Another recent study used a similar adaptive training paradigm to train participants on the orientation change detection tasks, which found decreased mean recall error in an orientation delay estimation task (Wang & Qian, 2020). Because they did not use model-fitting methods to decompose the guessing rate and precision, it is unclear whether their training improved working capacity, precision, or both. Interestingly, we also found the low-load nonadaptive training led to an improvement in color WM precision and color perception. These results were not surprising because our adaptive paradigm manipulated set size and may encourage capacity effect, whereas the low-load, nonadaptive paradigm may emphasize the color perception of a single item.

Consistent with previous studies that found negligible far transfer effects (Kassai et al., 2019; Melby-Lervåg & Hulme, 2016), in the present study, no transfer to other visual WM tasks (such as spatial 2-back and complex span tasks), an attentional filtering task (a hybrid orientation

task with targets and distractors), or a general intelligence test (Raven reasoning task) was observed. These results emphasize the distinct mechanisms of different WM components (such as storage and manipulation; Li et al., 2017; Shipstead, Redick, Hicks, & Engle, 2012; Kane et al., 2004) and of WM and higher-level reasoning processes (Krawczyk, 2012; Melrose, Poulin, & Stern, 2007). More importantly, the present study revealed that simultaneous changes in the stimulus and task structure per se imposed additional constraints on training transfer. Previous adaptive WM training studies have reported successful transfer between stimuli (color, orientation, and shape) when the same WM tasks were adapted (Norris et al., 2019; Buschkuhl et al., 2017), as well as between change detection tasks and delay estimation tasks when the same stimuli were adopted (Wang & Qian, 2020). Still, these studies either did not include a control group (Buschkuhl et al., 2017) or used no-training control groups (Wang & Qian, 2020; Norris et al., 2019); it is thus unclear whether these transfer effects reflect some general expectation or practice effect.

It is worth noting that the current study found a main effect of training in the transfer effect. Nevertheless, without a significant group by test interaction, our result did not provide reliable evidence to support the transfer effect. Indeed, post hoc tests only revealed a weak (although significant) increase in orientation WM task for the training group, but no significant effect for the control group. As a result, the main effect could simply reflect common expectation and/or practice effects in both groups, and the lack of interaction effect could partly be due to a relatively weak training effect. Meanwhile, the low-load, nonadaptive training did not improve the color WM capacity. This null training effect in the control group was consistent with previous studies (Dunning & Holmes, 2014; Holmes et al., 2009) and provided additional evidence to support the lack of transfer.

Our limited training transfer effect was predicted by similarity-based transfer theories, which suggest that simultaneous changes in stimulus and task structure reduce the number of common features between tasks, impeding transfer (Constantinidis & Klingberg, 2016; Minear et al., 2016). Although previous studies revealed a highly correlated performance between the delay estimation task and change detection task with the same stimuli (Xie & Zhang, 2017; Ayeroff, Gill, & Alvarez, 2012), we found no significant correlation between the WM capacity in the color delay estimation task and orientation change detection task, lending support to the above hypothesis. Moreover, although the contralateral delay activities and alpha power changes showed memory load effects in both the color change detection task and orientation delay estimation task (Adam, Robison, & Vogel, 2018; Vogel & Machizawa, 2004), we found dissociated neural indices that reflected the WM capacity in both the color delay estimation task and orientation change detection task. In particular, parietal theta power suppression during the early

delay period reflected individual WM capacity for color recall, whereas the temporoparietal alpha power increase during the late delay period reflected the WM capacity for orientation change detection. Moreover, training only increased parietal theta power suppression in the color recall task. Taken together, these results suggest that the simultaneous changes of stimulus and task structure would modulate the cognitive and neural mechanisms of WM tasks and introduce additional limits for the training transfer.

The EEG results also contribute to our understanding of the neural mechanisms of WM capacity. The specific role of early parietal theta oscillation in the color delay estimation task was consistent with previous EEG and noninvasive brain stimulation studies. For example, transcranial alternating current stimulation studies revealed that parietal theta-band stimulation improved WM capacity in color change detection tasks (Bender, Romei, & Sauseng, 2019; Wolinski, Cooper, Sauseng, & Romei, 2018; Jaušovec & Jaušovec, 2014). Meanwhile, simultaneous EEG recordings revealed significant changes in theta oscillation during the early delay period (Jaušovec & Jaušovec, 2014). Future studies could further examine the functional role of theta oscillation in orientation WM. In contrast, the current study found that the temporoparietal alpha oscillation tracked the capacity of the orientation change detection task, which is consistent with the role of temporoparietal alpha oscillation in representing and binding spatial information. For example, the parietal and temporal cortex (Manohar, Zokaei, Fallon, Vogels, & Husain, 2019; Parra, Della Sala, Logie, & Morcom, 2014) and in particular the posterior alpha oscillations (Zhang, Qiu, Zhang, Han, & Fang, 2014) have been implicated in binding objects with the spatial information. Meanwhile, accumulating studies have found that the posterior alpha oscillations played a critical role in maintaining spatial information during WM delay (van Ede, Niklaus, & Nobre, 2017; Foster, Sutterer, Serences, Vogel, & Awh, 2016; Samaha et al., 2016). Recent studies have decoded item-specific representations for orientations from posterior alpha oscillations in both delay estimation task (Bae & Luck, 2019) and change detection task (Barbosa, Babushkin, Temudo, Sreenivasan, & Compte, 2021), whereas the decoding accuracy was lower when less spatial information was maintained (Bae, 2021; Bae & Luck, 2018). Unlike colors, orientations essentially contain spatial information. In addition, there is evidence that the binding of spatial locations and orientations might require extra binding effort likely due to their shared spatial features (Cai, Fulvio, Yu, Sheldon, & Postle, 2020). Future studies could further examine the functional role of alpha oscillation in color WM. Given the complexity of stimuli type and task structure, future works should test the stability and generalization of these neural indices more thoroughly.

For the neural indexes for WM capacities, although we observed that parietal-occipital slow waves and alpha suppression tracked WM capacity at the group level in both

color and orientation WM tasks, we did not replicate the correlation between these two signals and either WM capacity at the individual level (Fukuda et al., 2015). One possibility of this inconsistency could be that the current study used color recall and orientation change detection tasks, whereas Fukuda's study used a color change detection task. And our results suggest that parietal-occipital slow waves and alpha suppression may be sensitive to both the stimulus type and task structure. However, we cannot exclude other possibilities such as individual differences. These results remind us that it could be challenging to build well-established neural markers for WM capacities and more replication studies for neural indexes for WM capacity should be encouraged in the future.

Several important questions should be addressed in future work. First, future studies should further investigate the cognitive and neural processes that underlie each WM task, which could help to understand the presence or absence of the transfer effects. Second, in addition to the similarity between the trained and transfer tasks, other factors could affect the transfer effect. For example, recent cognitive routine theory posits that transfer relies on learning a new cognitive routine during training and adopting the new routine in the untrained tasks. According to this theory, transfer effects will be greater when training with unfamiliar paradigms (e.g., nonserial visual change detection task) than well-established paradigms (serial digital recall task; Gathercole et al., 2019; Norris et al., 2019). Future studies should examine how the acquisition of cognitive skills and the similarity between trained and transfer tasks jointly influence the transfer effect. Finally, future studies should investigate how the length of training and the inclusion of multiple training tasks impact the transfer effect.

In conclusion, by combining model fitting with EEG recordings, the present study revealed that simultaneous changes in the stimulus and task structure could significantly change the cognitive and neural mechanisms underlying VWM capacity and introduced additional limitations on the transfer effect of WM training. These results provide important insights into the cognitive and neural mechanisms underlying WM training and the transfer effect, which has significant theoretical and practical implications.

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Ying Cai: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Software; Writing—

Original draft; Writing—Review & editing. Can Yang: Formal analysis; Investigation. Sisi Wang: Formal analysis; Resources; Writing—Review & editing. Gui Xue: Conceptualization; Funding acquisition; Supervision; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: $M/M = .463$, $W/M = .259$, $M/W = .148$, and $W/W = .13$.

REFERENCES

- Adam, K. C. S., Robison, M. K., & Vogel, E. K. (2018). Contralateral delay activity tracks fluctuations in working memory performance. *Journal of Cognitive Neuroscience*, 30, 1229–1240. https://doi.org/10.1162/jocn_a_01233, PubMed: 29308988
- Au, J., Sheehan, E., Tsai, N., Duncan, G. J., Buschkuhl, M., & Jaeggi, S. M. (2015). Improving fluid intelligence with training on working memory: A meta-analysis. *Psychonomic Bulletin & Review*, 22, 366–377. <https://doi.org/10.3758/s13423-014-0699-x>, PubMed: 25102926
- Ayeroff, E., Gill, J., & Alvarez, G. (2012). Estimating the quantity and quality of working memory representations with continuous report versus change detection. *Journal of Vision*, 12, 345. <https://doi.org/10.1167/12.9.345>
- Bae, G.-Y. (2021). Neural evidence for categorical biases in location and orientation representations in a working memory task. *Neuroimage*, 240, 118366. <https://doi.org/10.1016/j.neuroimage.2021.118366>, PubMed: 34242785
- Bae, G.-Y., & Luck, S. J. (2018). Dissociable decoding of spatial attention and working memory from EEG oscillations and sustained potentials. *Journal of Neuroscience*, 38, 409–422. <https://doi.org/10.1523/JNEUROSCI.2860-17.2017>, PubMed: 29167407
- Bae, G.-Y., & Luck, S. J. (2019). What happens to an individual visual working memory representation when it is interrupted? *British Journal of Psychology*, 110, 268–287. <https://doi.org/10.1111/bjop.12339>, PubMed: 30069870
- Bahramisharif, A., Jensen, O., Jacobs, J., & Lisman, J. (2018). Serial representation of items during working memory maintenance at letter-selective cortical sites. *PLoS Biology*, 16, e2003805. <https://doi.org/10.1371/journal.pbio.2003805>, PubMed: 30110320
- Barbosa, J., Babushkin, V., Temudo, A., Sreenivasan, K. K., & Compte, A. (2021). Across-area synchronization supports feature integration in a biophysical network model of working memory. *Frontiers in Neural Circuits*, 15, 716965. <https://doi.org/10.3389/fncir.2021.716965>, PubMed: 34616279
- Bays, P. M. (2018). Reassessing the evidence for capacity limits in neural signals related to working memory. *Cerebral Cortex*, 28, 1432–1438. <https://doi.org/10.1093/cercor/bhx351>, PubMed: 29329385
- Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, 321, 851–854. <https://doi.org/10.1126/science.1158023>, PubMed: 18687968
- Bender, M., Romei, V., & Sauseng, P. (2019). Slow theta tACS of the right parietal cortex enhances contralateral visual working memory capacity. *Brain Topography*, 32, 477–481. <https://doi.org/10.1007/s10548-019-00702-2>, PubMed: 30694422
- Buschkuhl, M., Jaeggi, S. M., Mueller, S. T., Shah, P., & Jonides, J. (2017). Training change detection leads to substantial task-specific improvement. *Journal of Cognitive Enhancement*, 1, 419–433. <https://doi.org/10.1007/s41465-017-0055-y>
- Cai, Y., Fulvio, J. M., Yu, Q., Sheldon, A. D., & Postle, B. R. (2020). The role of location-context binding in nonspatial visual working memory. *eNeuro*, 7, ENEURO.0430-20.2020. <https://doi.org/10.1523/ENEURO.0430-20.2020>, PubMed: 33257529
- Cai, Y., Urgolites, Z., Wood, J., Chen, C., Li, S., Chen, A., et al. (2018). Distinct neural substrates for visual short-term memory of actions. *Human Brain Mapping*, 39, 4119–4133. <https://doi.org/10.1002/hbm.24236>, PubMed: 29947094
- Chein, J. M., & Morrison, A. B. (2010). Expanding the mind's workspace: Training and transfer effects with a complex working memory span task. *Psychonomic Bulletin & Review*, 17, 193–199. <https://doi.org/10.3758/PBR.17.2.193>, PubMed: 20382919
- Constantinidis, C., & Klingberg, T. (2016). The neuroscience of working memory capacity and training. *Nature Reviews Neuroscience*, 17, 438–449. <https://doi.org/10.1038/nrn.2016.43>, PubMed: 27225070
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, 24, 87–114. <https://doi.org/10.1017/S0140525X01003922>, PubMed: 11515286
- Dahlin, E., Neely, A. S., Larsson, A., Backman, L., & Nyberg, L. (2008). Transfer of learning after updating training mediated by the striatum. *Science*, 320, 1510–1512. <https://doi.org/10.1126/science.1155466>, PubMed: 18556560
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>, PubMed: 15102499
- Ding, X., Zhao, Y., Wu, F., Lu, X., Gao, Z., & Shen, M. (2015). Binding biological motion and visual features in working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 41, 850–865. <https://doi.org/10.1037/xhp0000061>, PubMed: 25893683
- Dunning, D. L., & Holmes, J. (2014). Does working memory training promote the use of strategies on untrained working

- memory tasks? *Memory & Cognition*, *42*, 854–862. <https://doi.org/10.3758/s13421-014-0410-5>, PubMed: 24748348
- Foster, J. J., Sutterer, D. W., Serences, J. T., Vogel, E. K., & Awh, E. (2016). The topography of alpha-band activity tracks the content of spatial working memory. *Journal of Neurophysiology*, *115*, 168–177. <https://doi.org/10.1152/jn.00860.2015>, PubMed: 26467522
- Foy, J. G., & Mann, V. A. (2014). Adaptive cognitive training enhances executive control and Visuospatial and verbal working memory in beginning readers. *International Economic Review*, *2*, 19–43. <https://doi.org/10.12735/ier.v2i2p19>
- Fukuda, K., Mance, I., & Vogel, E. K. (2015). Power modulation and event-related slow wave provide dissociable correlates of visual working memory. *Journal of Neuroscience*, *35*, 14009–14016. <https://doi.org/10.1523/JNEUROSCI.5003-14.2015>, PubMed: 26468201
- Gabrieli, J. D. E., Singh, J., Stebbins, G. T., & Goetz, C. G. (1996). Reduced working memory span in Parkinson's disease: Evidence for the role of frontostriatal system in working and strategic memory. *Neuropsychology*, *10*, 322–332. <https://doi.org/10.1037/0894-4105.10.3.321>
- Gaspar, J. G., Neider, M. B., Simons, D. J., McCarley, J. S., & Kramer, A. F. (2013). Change detection: Training and transfer. *PLoS One*, *8*, e67781. <https://doi.org/10.1371/journal.pone.0067781>, PubMed: 23840775
- Gathercole, S. E., Dunning, D. L., Holmes, J., & Norris, D. (2019). Working memory training involves learning new skills. *Journal of Memory and Language*, *105*, 19–42. <https://doi.org/10.1016/j.jml.2018.10.003>, PubMed: 31235992
- Goldman-Rakic, P. S. (1994). Working memory dysfunction in schizophrenia. *Journal of Neuropsychiatry and Clinical Neurosciences*, *6*, 348–357. <https://doi.org/10.1176/jnp.6.4.348>, PubMed: 7841806
- Hamel, R., & Schmittmann, V. D. (2006). The 20-minute version as a predictor of the Raven Advanced Progressive Matrices Test. *Educational and Psychological Measurement*, *66*, 1039–1046. <https://doi.org/10.1177/0013164406288169>
- Harrison, T. L., Shipstead, Z., Hicks, K. L., Hambrick, D. Z., Redick, T. S., & Engle, R. W. (2013). Working memory training may increase working memory capacity but not fluid intelligence. *Psychological Science*, *24*, 2409–2419. <https://doi.org/10.1177/0956797613492984>, PubMed: 24091548
- Holmes, J., Gathercole, S. E., & Dunning, D. L. (2009). Adaptive training leads to sustained enhancement of poor working memory in children. *Developmental Science*, *12*, F9–F15. <https://doi.org/10.1111/j.1467-7687.2009.00848.x>, PubMed: 19635074
- Jordan, A. D., Cooke, K. A., Moored, K. D., Katz, B., Buschkuhl, M., Jaeggi, S. M., et al. (2020). Neural correlates of working memory training: Evidence for plasticity in older adults. *Neuroimage*, *217*, 116887. <https://doi.org/10.1016/j.neuroimage.2020.116887>, PubMed: 32376302
- Jaeggi, S. M., Buschkuhl, M., Jonides, J., & Perrig, W. J. (2008). Improving fluid intelligence with training on working memory. *Proceedings of the National Academy of Sciences, U.S.A.*, *105*, 6829–6833. <https://doi.org/10.1073/pnas.0801268105>, PubMed: 18443283
- Jaeggi, S. M., Buschkuhl, M., Jonides, J., & Shah, P. (2011). Short- and long-term benefits of cognitive training. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 10081–10086. <https://doi.org/10.1073/pnas.1103228108>, PubMed: 21670271
- Jaušovec, N., & Jaušovec, K. (2014). Increasing working memory capacity with theta transcranial alternating current stimulation (tACS). *Biological Psychology*, *96*, 42–47. <https://doi.org/10.1016/j.biopsycho.2013.11.006>, PubMed: 24291565
- Jiang, Y. V., Makovski, T., & Shim, W. M. (2009). Visual memory for features, conjunctions, objects, and locations. In J. R. Brockmole (Ed.), *The visual world in memory* (pp. 33–65). Psychology Press.
- Kane, M. J., Tuholski, S. W., Hambrick, D. Z., Wilhelm, O., Payne, T. W., & Engle, R. W. (2004). The generality of working memory capacity: A latent-variable approach to verbal and visuospatial memory span and reasoning. *Journal of Experimental Psychology: General*, *133*, 189–217. <https://doi.org/10.1037/0096-3445.133.2.189>, PubMed: 15149250
- Kassai, R., Futo, J., Demetrovics, Z., & Takacs, Z. K. (2019). A meta-analysis of the experimental evidence on the near- and far-transfer effects among children's executive function skills. *Psychological Bulletin*, *145*, 165–188. <https://doi.org/10.1037/bul0000180>, PubMed: 30652908
- Katz, B., Shah, P., & Meyer, D. E. (2018). How to play 20 questions with nature and lose: Reflections on 100 years of brain-training research. *Proceedings of the National Academy of Sciences, U.S.A.*, *115*, 9897–9904. <https://doi.org/10.1073/pnas.1617102114>, PubMed: 30275315
- Klingberg, T. (2010). Training and plasticity of working memory. *Trends in Cognitive Sciences*, *14*, 317–324. <https://doi.org/10.1016/j.tics.2010.05.002>, PubMed: 20630350
- Klingberg, T., Forssberg, H., & Westerberg, K. (2002). Training of working memory in children with ADHD. *Journal of Clinical and Experimental Neuropsychology*, *24*, 781–791. <https://doi.org/10.1076/j.cen.24.6.781.8395>, PubMed: 12424652
- Krawczyk, D. C. (2012). The cognition and neuroscience of relational reasoning. *Brain Research*, *1428*, 13–23. <https://doi.org/10.1016/j.brainres.2010.11.080>, PubMed: 21129363
- Ku, Y., Bodner, M., & Zhou, Y.-D. (2015). Prefrontal cortex and sensory cortices during working memory: Quantity and quality. *Neuroscience Bulletin*, *31*, 175–182. <https://doi.org/10.1007/s12264-014-1503-7>, PubMed: 25732526
- Lee, E.-Y., Cowan, N., Vogel, E. K., Rolan, T., Valle-Inclán, F., & Hackley, S. A. (2010). Visual working memory deficits in patients with Parkinson's disease are due to both reduced storage capacity and impaired ability to filter out irrelevant information. *Brain*, *133*, 2677–2689. <https://doi.org/10.1093/brain/awq197>, PubMed: 20688815
- Lee, J., & Park, S. (2005). Working memory impairments in schizophrenia: A meta-analysis. *Journal of Abnormal Psychology*, *114*, 599–611. <https://doi.org/10.1037/0021-843X.114.4.599>, PubMed: 16351383
- Li, S., Cai, Y., Liu, J., Li, D., Feng, Z., Chen, C., et al. (2017). Dissociated roles of the parietal and frontal cortices in the scope and control of attention during visual working memory. *Neuroimage*, *149*, 210–219. <https://doi.org/10.1016/j.neuroimage.2017.01.061>, PubMed: 28131893
- Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience & Biobehavioral Reviews*, *62*, 100–108. <https://doi.org/10.1016/j.neubiorev.2016.01.003>, PubMed: 26802451
- Manohar, S. G., Zokaei, N., Fallon, S. J., Vogels, T. P., & Husain, M. (2019). Neural mechanisms of attending to items in working memory. *Neuroscience & Biobehavioral Reviews*, *101*, 1–12. <https://doi.org/10.1016/j.neubiorev.2019.03.017>, PubMed: 30922977
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>, PubMed: 17517438
- Melby-Lervåg, M., & Hulme, C. (2016). There is no convincing evidence that working memory training is effective: A reply to Au et al. (2014) and Karbach and Verhaeghen (2014). *Psychonomic Bulletin & Review*, *23*, 324–330. <https://doi.org/10.3758/s13423-015-0862-z>, PubMed: 26082279

- Melby-Lervåg, M., Redick, T. S., & Hulme, C. (2016). Working memory training does not improve performance on measures of intelligence or other measures of “far transfer.” *Perspectives on Psychological Science, 11*, 512–534. <https://doi.org/10.1177/1745691616635612>, PubMed: 27474138
- Melrose, R. J., Poulin, R. M., & Stern, C. E. (2007). An fMRI investigation of the role of the basal ganglia in reasoning. *Brain Research, 1142*, 146–158. <https://doi.org/10.1016/j.brainres.2007.01.060>, PubMed: 17320049
- Minear, M., Brasher, F., Guerrero, C. B., Brasher, M., Moore, A., & Sukeena, J. (2016). A simultaneous examination of two forms of working memory training: Evidence for near transfer only. *Memory & Cognition, 44*, 1014–1037. <https://doi.org/10.3758/s13421-016-0616-9>, PubMed: 27129921
- Norris, D. G., Hall, J., & Gathercole, S. E. (2019). Can short-term memory be trained? *Memory & Cognition, 47*, 1012–1023. <https://doi.org/10.3758/s13421-019-00901-z>, PubMed: 30815843
- Parra, M. A., Della Sala, S., Logie, R. H., & Morcom, A. M. (2014). Neural correlates of shape–color binding in visual working memory. *Neuropsychologia, 52*, 27–36. <https://doi.org/10.1016/j.neuropsychologia.2013.09.036>, PubMed: 24120612
- Pergher, V., Wittevrongel, B., Tournoy, J., Schoenmakers, B., & Van Hulle, M. M. (2018). N-back training and transfer effects revealed by behavioral responses and EEG. *Brain and Behavior, 8*, e01136. <https://doi.org/10.1002/brb3.1136>, PubMed: 30350357
- Postle, B. R., Stern, C. E., Rosen, B. R., & Corkin, S. (2000). An fMRI investigation of cortical contributions to spatial and nonspatial visual working memory. *Neuroimage, 11*, 409–423. <https://doi.org/10.1006/nimg.2000.0570>, PubMed: 10806028
- Redick, T. S. (2019). The hype cycle of working memory training. *Current Directions in Psychological Science, 28*, 423–429. <https://doi.org/10.1177/0963721419848668>, PubMed: 31814661
- Redick, T. S., Shipstead, Z., Harrison, T. L., Hicks, K. L., Fried, D. E., Hambrick, D. Z., et al. (2013). No evidence of intelligence improvement after working memory training: A randomized, placebo-controlled study. *Journal of Experimental Psychology: General, 142*, 359–379. <https://doi.org/10.1037/a0029082>, PubMed: 22708717
- Roggeman, C., Klingberg, T., Feenstra, H. E. M., Compte, A., & Almeida, R. (2014). Trade-off between capacity and precision in visuospatial working memory. *Journal of Cognitive Neuroscience, 26*, 211–222. https://doi.org/10.1162/jocn_a_00485, PubMed: 24047380
- Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha–gamma versus theta–gamma codes for distinct WM information? *Trends in Cognitive Sciences, 18*, 16–25. <https://doi.org/10.1016/j.tics.2013.10.010>, PubMed: 24268290
- Samaha, J., Sprague, T. C., & Postle, B. R. (2016). Decoding and reconstructing the focus of spatial attention from the topography of alpha-band oscillations. *Journal of Cognitive Neuroscience, 28*, 1090–1097. https://doi.org/10.1162/jocn_a_00955, PubMed: 27003790
- Sandberg, P., & Stigsdotter Neely, A. (2016). Long-term effects of executive process training in young and old adults. *Neuropsychological Rehabilitation, 26*, 761–782. <https://doi.org/10.1080/09602011.2015.1108205>, PubMed: 26599201
- Schneegans, S., & Bays, P. M. (2016). No fixed item limit in visuospatial working memory. *Cortex, 83*, 181–193. <https://doi.org/10.1016/j.cortex.2016.07.021>, PubMed: 27565636
- Shen, M., Gao, Z., Ding, X., Zhou, B., & Huang, X. (2014). Holding biological motion information in working memory. *Journal of Experimental Psychology: Human Perception and Performance, 40*, 1332–1345. <https://doi.org/10.1037/a0036839>, PubMed: 24842069
- Shipstead, Z., Redick, T. S., Hicks, K. L., & Engle, R. W. (2012). The scope and control of attention as separate aspects of working memory. *Memory, 20*, 608–628. <https://doi.org/10.1080/09658211.2012.691519>, PubMed: 22734653
- Soveri, A., Antfolk, J., Karlsson, L., Salo, B., & Laine, M. (2017). Working memory training revisited: A multi-level meta-analysis of n-back training studies. *Psychonomic Bulletin & Review, 24*, 1077–1096. <https://doi.org/10.3758/s13423-016-1217-0>, PubMed: 28116702
- Soveri, A., Karlsson, E. P. A., Waris, O., Grönholm-Nyman, P., & Laine, M. (2017). Pattern of near transfer effects following working memory training with a dual n-back task. *Experimental Psychology, 64*, 240–252. <https://doi.org/10.1027/1618-3169/a000370>, PubMed: 28922999
- Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Developmental Science, 10*, 89–96. <https://doi.org/10.1111/j.1467-7687.2007.00569.x>, PubMed: 17181705
- Taatgen, N. A. (2013). The nature and transfer of cognitive skills. *Psychological Review, 120*, 439–471. <https://doi.org/10.1037/a0033138>, PubMed: 23750831
- Unsworth, N., Heitz, R. P., Schrock, J. C., & Engle, R. W. (2005). An automated version of the operation span task. *Behavior Research Methods, 37*, 498–505. <https://doi.org/10.3758/BF03192720>, PubMed: 16405146
- van Ede, F., Niklaus, M., & Nobre, A. C. (2017). Temporal expectations guide dynamic prioritization in visual working memory through attenuated α oscillations. *Journal of Neuroscience, 37*, 437–445. <https://doi.org/10.1523/JNEUROSCI.2272-16.2016>, PubMed: 28077721
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428*, 748–751. <https://doi.org/10.1038/nature02447>, PubMed: 15085132
- Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature, 438*, 500–503. <https://doi.org/10.1038/nature04171>, PubMed: 16306992
- von Bastian, C. C., & Oberauer, K. (2013). Distinct transfer effects of training different facets of working memory capacity. *Journal of Memory and Language, 69*, 36–58. <https://doi.org/10.1016/j.jml.2013.02.002>
- Wang, K., & Qian, J. (2020). Training with high perceptual difficulty improves the capacity and fidelity of internal representation in VWM. *Psychological Research, 85*, 2408–2419. <https://doi.org/10.1007/s00426-020-01404-2>, PubMed: 32809086
- Wang, S., Itthipuripat, S., & Ku, Y. (2019). Electrical stimulation over human posterior parietal cortex selectively enhances the capacity of visual short-term memory. *Journal of Neuroscience, 39*, 528–536. <https://doi.org/10.1523/JNEUROSCI.1959-18.2018>, PubMed: 30459222
- Wang, S., Itthipuripat, S., & Ku, Y. (2020). Encoding strategy mediates the effect of electrical stimulation over posterior parietal cortex on visual short-term memory. *Cortex, 128*, 203–217. <https://doi.org/10.1016/j.cortex.2020.03.005>, PubMed: 32361592
- Weicker, J., Villringer, A., & Thöne-Otto, A. (2016). Can impaired working memory functioning be improved by training? A meta-analysis with a special focus on brain injured patients. *Neuropsychology, 30*, 190–212. <https://doi.org/10.1037/neu0000227>, PubMed: 26237626
- Wolinski, N., Cooper, N. R., Sauseng, P., & Romei, V. (2018). The speed of parietal theta frequency drives visuospatial working memory capacity. *PLoS Biology, 16*, e2005348. <https://doi.org/10.1371/journal.pbio.2005348>, PubMed: 29538384

- Wood, J. N. (2007). Visual working memory for observed actions. *Journal of Experimental Psychology: General*, *136*, 639–652. <https://doi.org/10.1037/0096-3445.136.4.639>, PubMed: 17999576
- Wood, J. N. (2008). Visual memory for agents and their actions. *Cognition*, *108*, 522–532. <https://doi.org/10.1016/j.cognition.2008.02.012>, PubMed: 18472092
- Wood, J. N. (2011). A core knowledge architecture of visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 357–381. <https://doi.org/10.1037/a0021935>, PubMed: 21463083
- Xie, W., & Zhang, W. (2017). Familiarity speeds up visual short-term memory consolidation. *Journal of Experimental Psychology: Human Perception and Performance*, *43*, 1207–1221. <https://doi.org/10.1037/xhp0000355>, PubMed: 28287761
- Xu, Z., Adam, K. C. S., Fang, X., & Vogel, E. K. (2018). The reliability and stability of visual working memory capacity. *Behavior Research Methods*, *50*, 576–588. <https://doi.org/10.3758/s13428-017-0886-6>, PubMed: 28389852
- Yuan, K., Steedle, J., Shavelson, R., Alonzo, A., & Oppezzo, M. (2006). Working memory, fluid intelligence, and science learning. *Educational Research Review*, *1*, 83–98. <https://doi.org/10.1016/j.edurev.2006.08.005>
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, *453*, 233–235. <https://doi.org/10.1038/nature06860>, PubMed: 18385672
- Zhang, X., Qiu, J., Zhang, Y., Han, S., & Fang, F. (2014). Misbinding of color and motion in human visual cortex. *Current Biology*, *24*, 1354–1360. <https://doi.org/10.1016/j.cub.2014.04.045>, PubMed: 24856212
- Zhao, Y., Kuai, S., Zanto, T. P., & Ku, Y. (2020). Neural correlates underlying the precision of visual working memory. *Neuroscience*, *425*, 301–311. <https://doi.org/10.1016/j.neuroscience.2019.11.037>, PubMed: 31812661

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