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Consolidation time affects performance and neural activity during visual working memory

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ABSTRACT

We tested the effects of variation of stimulus onset asynchrony (SOA) on visual working memory (WM) performance across different load levels and the underlying brain activation patterns using functional magnetic resonance imaging (fMRI) in 48 healthy participants. Participants were instructed to memorise arrays of coloured squares and had to perform a match/non-match judgement on a probe stimulus after a jittered delay. We presented visual pattern masks at four SOAs after the offset of the memory array (100 ms, 200 ms, 400 ms, and 800 ms). Memory performance decreased with increased load and shortened SOA. Brain activation data showed significant effects of load (during encoding and retrieval), SOA (retrieval) and an interaction of load by SOA (encoding), mainly in frontal and parietal areas. There was also a direct relationship between successfully stored items and activation in the right inferior parietal lobule and the left middle frontal gyrus. The neurobehavioral results suggest that the frontal regions, together with the inferior parietal lobe, are associated with successful WM performance, especially under the most challenging conditions of high load and short SOAs.

1. Introduction

Working memory (WM) capacity is considered to be a fundamental basis for a number of higher order cognitive functions, including language and learning (Baddeley, 2003). Visual WM, the "visual-spatial sketchpad" (Baddeley, 2003), integrates visual and spatial information into a unitary visual-spatial representation of objects. However, more recent work has suggested that visual and spatial memory systems are separate (Salway and Logie, 1995; Mohr et al., 2006; Linden, 2007). The newer formulation is based on the observation that dual tasks requiring the storage of both visual and spatial information can be performed without any additional cost in comparison with the storage of one type of information (visual or spatial) (Mohr and Linden, 2005).

The capacity of visual WM is limited by a number of factors, including the number of objects and features (e.g. form, colour, texture, location) and the time span available for the stimulus onset asynchrony (SOA) of the items (Alvarez and Cavanagh, 2004; Davis and Holmes, 2005). The concept of memory consolidation holds that perceptual information will be transformed into a durable WM representation that can survive the presentation of new sensory inputs (Shapiro and Miller, 2011).

As suggested elsewhere (Jolicoeur and Dell'Acqua, 1998; Vogel et al., 2006), consolidation is an important bottleneck for memory encoding. Several studies have suggested that it takes approximately 50 ms for a single item to be stored in WM (Luck and Vogel, 1997; Giesbrecht and Di Lollo, 1998; (Dell'Acqua et al., 2010) and that higher load of stimuli demands more cognitive effort (Jolicoeur and Dell'Acqua, 1998; Vogel et al., 2006; Ling et al., 2011). In the current study, we systematically tested the effects of varied SOA times on the visual WM performance and its underlying neural pattern.

Current knowledge about the functional pattern underlying storage processes within memory systems indicates that the different periods of a short-term memory task (encoding, maintenance, and retrieval) require distinct involvements of brain regions. For encoding and maintaining visuospatial information within memory, an increased recruitment of attention-associated

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areas within the parietal and frontal cortex has been identified as important (Fusser et al., 2011; Ling et al., 2011). During retrieval, the inferior portion of the ventro-lateral prefrontal cortex shows increased activity in contrast to baseline. For different load levels, several studies have indicated that prefrontal cortex activity differs depending on the task phase (Linden et al., 2003). However, the effect of limited or varied time for memory consolidation on task-related functional activation patterns has not yet been systematically investigated with functional imaging.

In the present study, we examined the number of successfully stored items, reaction time, and underlying neuronal activity patterns in a visual change detection task. We hypothesised that a shortened SOA time and higher load would be associated with a change in brain-activity pattern within the WM functional network. In particular, we predicted that increased demand during SOA might lead to a differential activation pattern of parts of the WM network.

2. Methods

2.1. Participants

We included 48 right-handed healthy participants (mean age=28.41 years, S.D.=8.21; range: 21–54; 23 females, 25 males) who were free of psychiatric disorders according to DSM-IV criteria (see Table 1 for further details). We ruled out syndromal Axis I or II disorders using the Structured Clinical Interview for DSM-IV (SCID-I and SCID-II; Wittchen et al., 1996). We also administered a number of symptom scales, the Beck Depression Inventory II for the assessment of depressive symptoms (BDI II; Kuhner et al., 2007), the German version of the Revised Hallucination Scale for the assessment of hallucinations (RHS; Morrison et al., 2002) and the Symptom Checklist of Derogatis (SCL-90-R; Franke, 2002) for the assessment of general psychopathology. For the SCL-90-R, we selected the scores for the subscale *depression* (SCL-90-R DEP) and the *global severity index*. We computed descriptive statistics (means, standard deviations, and range) for the scores of the clinical (BDI II, SCL-90-R, and RHS) tests for all participants (see Table 1 for further details). All tests indicated that none of the participants suffered from any psychiatric disorder, and none of the participants had any family history for a psychiatric disorder. Results of additional screening tests results are presented in the Supplemental material (Table S4).

Further exclusion criteria for participants were left-handedness, current drug abuse, neurological diseases, any history of psychiatric disorders including Axis I and Axis II disorders according to DSM-IV, and an inability to provide informed consent.

The anatomical magnetic resonance imaging (MRI) scans were reviewed by a neuroradiologist, who did not identify any pathological processes. Participants were provided with a description of the study and gave written informed consent before the study began. Experimental procedures were approved by the ethical board of the Medical Department of Goethe-University, Frankfurt/Main, Germany.

2.2. Data acquisition and image processing

All participants underwent functional and anatomical imaging on a Siemens Magnetom Allegra 3 T MRI system (Siemens Medical Systems, Erlangen, Germany) at the Frankfurt University Brain Imaging Center, Frankfurt/Main, Germany. The session included four functional scans of approximately 10 min (echoplanar imaging sequences, 465 volumes, voxel size: $3 \times 3 \times 3$ mm^3, repetition time=2000 ms, echo time=30 ms, 33 slices, slice thickness=3 mm, dist. factor: 20%, and flip angle: 90°) in a paradigm designed to assess visual WM. During the functional scans, participants were instructed to look at a fixation cross in the middle of the screen. Participants were asked not to verbalise the material. Each run included 20 trials of the WM task (see Fig. 1). The stimulus material was randomly distributed across runs. A mirror was fixed on the head coil to present the stimulus material in the scanner. All stimuli were presented on a video monitor with a grey background. We synchronized the stimulus presentation with the fMRI sequences at the beginning of each trial using MRI pulses that triggered the ongoing presentation of stimuli in the Presentation® software.

After the second functional scan, we acquired a high-resolution T1-weighted MDEFT sequence (176 slices, $1 \times 1 \times 1$ mm^3) (Deichmann et al., 2004) for anatomical measurement covering the whole brain. The anatomical measurement was followed by the third and fourth functional scans.

Table 1
Sociodemographic and clinical characteristics of the participants (n=48).

Variable	*M* (S.D.)	Range (min.–max.)	Percentils 25/75%
Age	28.41 (8.21)	33 (21–54)	22/34
Gender	23 *F*/25 *M*		
Handedness	All right handed		
RHS mean score	25.39 (4.61)	19 (20–39)	22/28
BDI II	2.79 (3.84)	8 (1–9)	1/3
SCL-90-R global severity index	12.28 (2.45)	7 (10–17)	10/14
SCL-90-R subscale depression	0.16 (0.20)	0.68 (0.02–0.71)	0.10/0.61

The abbreviations are as follows: S.D.=standard deviation, *M*=mean, RHS=Revised Hallucination Scale (Morrison et al., 2002), SCL-90-R=Symptom-Checklist by Derogatis, BDI II=Beck Depression Inventory.

2.3. Functional imaging

2.3.1. Functional imaging: procedure

All functional scans started with a baseline condition that consisted of a black fixation cross in the middle of the screen. The fixation cross was continuously presented during the whole measurement. Before each task, the black fixation cross blinked red for 500 ms to announce the start of a new task and to ensure that the attention of the participant was on the screen. Between each task, an inter-stimulus interval (ISI) (black fixation cross) with jittered duration (14–16 s) was presented to prevent participants from continued retrieval of WM tasks, to ensure that participants persisted with their attention to the screen, and to provide a suitable baseline for the subsequent WM conditions. Each functional scan included 20 visual WM trials; and each trial consisted of three task periods, containing encoding, maintenance and retrieval periods (see Fig. 1 for a detailed description of the time line of the current experiment). In total, 80 different trials of two conditions (condition 1: load: load 3/match, load 3/non-match, load 5/match, load 5/non-match) [each 20 trials], condition 2: SOA (100 ms, 200 ms, 400 ms, and 800 ms) were presented randomly. The different conditions were equally distributed over the whole measurement. The whole session lasted approximately 50 min.

2.3.2. Functional imaging: experimental paradigm

The *encoding* predictor included a memory array, a varied stimulus onset asynchrony (SOA), a pattern mask and a mask-to-probe-delay, lasting together 3000 ms.

The *memory array* consisted of three (load 3 condition) or five (load 5 condition) coloured squares of 50 mm^2, which were presented during encoding for 400 ms. There were eight possible positions for the squares circularly that were arranged around the fixation cross and selected randomly in each trial. The colour of the squares was randomly selected and varied between eight different colours (yellow, blue, green, pink, violet, red, white, and brown). None of the coloured squares were presented twice under one encoding condition.

The memory array was followed by a variable SOA (time before showing the pattern mask; 'SOA') and lasted randomly between 100 ms, 200 ms, 400 ms or 800 ms. The *pattern masks* lasted 200 ms and comprised a set of eight stimuli, consisting each of four small squares, centred over all of the memory array positions. The colours of the squares in the pattern masks were selected randomly.

It was followed by a jittered delay (delay I), which was variable and dependent on the presentation time for the memory array, SOA, pattern mask and the delay I together (=encoding, 3000 ms).

The encoding predictor was followed by the *maintenance predictor* (3000 ms), showing a fixation cross (ISI).

After that, a variable delay period (=*confound)* (delay III, delay IV) was presented to keep the presentation time between encoding and retrieval conditions constant. Altogether, the encoding period, the maintenance period and the delay (confound) lasted 12 s (in a jittered mode).

The *retrieval* period lasted for 3000 ms and contained the same stimulus material in the same colours as under the encoding condition (match), or it varied in the colour of one square (non-match). The location of the squares did not vary between encoding and retrieval. The participants were asked to decide whether the squares were the same or whether one of the squares differed in colour and to press a button with their right index finger for a match response, their middle finger for a non-match response. All participants were instructed to recollect the WM items as accurately and as quickly as possible (see Fig. 1).

2.3.3. Functional imaging: post-scanning debriefing

After the scan session, each subject underwent a post-scanning debriefing. Here, the participants were asked about their subjective attention and concentration during