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Running Head: Visual Working Memory in Amnesia

**Title: Visual Working Memory is Impaired when the
Medial Temporal Lobe is Damaged**

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Abstract

The canonical description of the role of the medial temporal lobes in memory is that short-term forms of memory (e.g. working memory -WM) are spared when the medial temporal lobe is damaged, but longer term forms of memory impaired. Tests used to assess this have typically had a heavy verbal component, potentially allowing explicit rehearsal strategies to maintain the working memory trace over the memory delay period. Here we test the hypothesis that the medial temporal lobe is necessary for visual WM when verbal rehearsal strategies are difficult to implement. In three patients with medial temporal lobe damage we found impairments in spatial, face, and color WM, at delays as short as 4 seconds. Impaired memory could not be attributed to memory load or perceptual problems. These findings suggest that the medial temporal lobes are critical for accurate visual working memory.

Visual Working Memory is Impaired when the Medial Temporal Lobe is Damaged

Bilateral damage to the hippocampus and related medial temporal lobe (MTL) structures (entorhinal, perirhinal, and parahippocampal cortex) causes severe memory impairments (Milner *et al.*, 1968). This impairment is characterized by profound explicit long-term memory deficits, but preservation of many types of procedural and implicit long-term memory and working memory (WM). The findings from patients with MTL amnesia were consistent with the multi-store view of memory (Atkinson & Shiffrin, 1971) - that short-term and long-term memory were separate psychological entities with separate underlying neural systems (A. Baddeley & Hitch, 1974) and thus these findings became the linch-pin evidence for the psychological distinction between short-term (henceforth termed working memory (WM) and long-term memory.

The evidence that is most frequently cited for intact WM after MTL damage comes from studies of verbal or phonological memory. For instance, WM for digits (Cave & Squire, 1992; Wickelgren, 1968) and words (Baddeley & Warrington, 1970) appears to be spared in MTL amnesia, whereas long-term memory for these types of stimuli is impaired (Cohen & Eichenbaum, 1993). In sum, there is consistent evidence that verbal WM does not rely on the MTL.

In contrast, evidence for intact *visual* WM with MTL damage is discussed more rarely because fewer studies have been conducted and those that exist provide a confusing mixture of results. For instance, Cave and Squire (1992) showed that MTL amnesics could accurately remember the location of a single dot or the shape of a single angle for up to 12 s. In contrast, other studies by Squire and colleagues have shown that MTL

amnesics can accurately remember a single novel shape for up to 25 s (Levy & Squire, 2005) but cannot accurately remember several novel shapes for more than 5 s (Buffalo *et al.*, 1998). Squire and colleagues (Levy & Squire, 2005) also reported that WM for a single face was intact in patients with damage restricted to the hippocampus but impaired at 7 s delays in patients with large MTL lesions. However, both normal controls and hippocampal patients were at ceiling performance, raising the question of whether hippocampal damage can cause face WM impairments when a more difficult (e.g. more sensitive) task is used. Milner and colleagues tested patients with MTL amnesia on incidental memory for objects or the location of objects and found intact object memory, but impaired location memory with right but not left MTL damage, when there was no delay interval (Smith & Milner, 1989). Interpretation of this finding in regards to spatial WM is complicated by the fact that the encoding manipulation was incidental and the task design encouraged encoding of object-location conjunctions.

What accounts for the discrepant visual WM results? We hypothesize that visual WM computations typically rely on an intact MTL but this neural route can be circumvented and accurate performance achieved on easy visual WM tasks by using a variety of strategies. For instance, if the task requires you to remember the visual location of a single dot (Cave & Squire, 1992), rather than holding the location in mind, you could choose instead to covertly orient the eyes, hand, or body toward the dot location, or you could simply rehearse a verbal description of the dot location (e.g. one inch from left, 2 inches down). In contrast, more difficult visual WM tasks, such as remembering several simultaneously presented locations, can only be mastered by holding in mind a representation of the stimuli.

Here we test MTL amnesics and age-matched controls in three experiments that require subjects to remember several locations (Experiment 1), a single face (Experiment 2), or several colors (Experiment 3) over 4 or 8 seconds (see Figure 1 for stimuli). Critical features of the present study include the use of tasks and stimuli that were difficult enough to avoid ceiling effects and that minimized the possibility that verbal strategies could be used to perform the task. If the MTL is necessary for accurate visual WM, patients should be impaired in all tasks. Alternatively, if the MTL is critical only for long-term forms of memory (Alvarez *et al.*, 1994; Cave & Squire, 1992) then no deficits should be observed.

Experiment 1: Results and Discussion

Figure 3 shows the results of our analysis. A repeated-measures ANOVA found a main effect of set size, $F(1, 1) = 16.06$, $p < .004$ due to worse performance with higher memory loads (21.9 mm off versus 38.6 mm off) and a main effect of group, $F(1, 8) = 12.44$, $p < .008$ due to worse performance by the amnesics. Whereas the control group deviated an average of 25.2 mm from the correct location, the amnesics deviated an average of 42.1 mm from the correct location. The interaction of set size and group, $F(1, 8) = 3.40$, $p = .10$, did not provide evidence of differentially poor performance at higher memory loads.

These results show that MTL amnesics have impaired visual WM for locations. This impairment was observed at both easy (set size 3, $p < .04$) and difficult (set size 6, $p < .02$) memory loads, discounting the explanation that the poorer performance by the amnesics was due to supra-span taxing of WM (Drachman & Arbit, 1966). However there is a trend, albeit, one that is not significant, towards an interaction between set size and group. It is possible that with more power, the interaction would become significant. The

presence of an interaction does not undermine our main point – that amnesics are worse than controls at both set sizes, however it does suggest that they may be additionally impaired by high memory load.

In the perceptual control task, average displacement error in the patient group was 6.6 mm whereas in the control group it was 5.7 mm. This difference was not significant ($p=.34$), showing that perceptual differences cannot account for the pattern of results exhibited on the visual WM task.

Experiment 2

Experiment 2 was designed to address two questions elicited by the findings of Experiment 1. First, are MTL amnesic's WM deficits limited to spatial WM? The hippocampus is intimately tied to spatial memory in rodents (O'Keefe & Nadel, 1978), and humans (Bohbot *et al.*, 1998; Holdstock *et al.*, 2000; Maguire *et al.*, 1996; Nunn *et al.*, 1998; Smith & Milner, 1989; Spiers *et al.*, 2001), so it is possible that the deficits found in Experiment 1 are specific to spatial forms of memory. A second question raised by the results of Experiment 1 is whether the results generalize to recognition tasks. Many prior studies have shown that MTL damage impairs recall more than recognition (Yonelinas, 2002) so it is possible that WM deficits will only be observed in recall tasks. Given that visual WM is commonly studied with recognition tasks (Jiang *et al.*, 2000; Luck & Vogel, 1997), it is important to test whether WM deficits exist for both recall and recognition tasks. Thus Experiment 2 tested whether the WM deficit observed in Experiment 1 generalizes to non-spatial stimuli and to a recognition task. On each trial, participants were required to remember a single face. Memory load was kept low because prior studies have shown that face WM is difficult, with memory capacity in college students

calculated to be about 1.5 faces (Eng *et al.*, 2005-in press). After a 4000 ms delay, a probe array containing either the same face or a different face was presented. The task was to indicate by keypress whether the face on the probe image matched the face held in memory.

Experiment 2: Results and Discussion

Figure 4 shows the results of our analysis. Corrected accuracy for the control group was .82, whereas for the patients it was .31. This difference was significant, $p < .003$. These results show that MTL amnesics can barely remember a single face. These results extend the results reported in Experiment 1 to non-spatial stimuli and to a recognition task and suggest that the MTL may have a general role in visual WM.

Were the visual WM results actually due to a face perception deficit? The perceptual analogue to the memory task showed that accuracy was high in the patient group (1.0) and the control group (.99). This difference was not significant ($p = .57$), showing that perceptual differences cannot account for the pattern of results exhibited on the visual WM task.

Experiment 3

In this last experiment, we again, assessed the generality of the WM deficits in amnesics by testing visual WM for color, using a task similar to that used by Jiang, Olson, and Chun (2000). In addition, we asked whether group differences in WM changed at lengthier delay intervals to assess the importance of memory decay. To test this, participants were asked to remember three colored squares over a delay of either 4000 or 8000 ms. Because we were interested in testing visual, not verbal WM, colors were chosen

that were difficult to verbalize.¹ If MTL amnesics have impaired color WM, performance should be lower at both delays. If their WM impairment is due to accelerated memory decay, their performance should be worse at the 8000 ms delay.

Results and Discussion

Figure 5 shows the results of our analysis. There was a main effect of group, $F(1, 8) = 5.4$, $p < .05$, due to lower overall performance by the amnesics ($M = .29$ versus $.66$) but the effect of delay, and the group X delay interaction was not significant (all F 's < 1 , n.s.).

Were the visual WM results actually due to a color perception deficit? In the perceptual analogue to the memory task, accuracy was high in the patient group (.98) and the control group (1.0). This difference was not significant ($p = .42$)², showing that perceptual differences cannot account for the pattern of results exhibited on the visual WM task.

General Discussion

In this paper we asked the simple question of whether visual working memory is reliant on the medial temporal lobe. The results of three experiments suggest that in order to remember visual information over a short delay interval, the MTL must be intact. In Experiment 1 patients with MTL amnesia had larger displacement errors when recalling

¹ Other investigators have used concurrent verbal memory loads to minimize the possibility that colors are remembered by their verbal labels (Luck & Vogel, 1997; Olson & Jiang, 2002). This type of task design is difficult to implement in older and patient populations and introduces additional variables that may confound the effect of interest. Because of this, we chose to limit verbal encoding by instructing study participants to remember the stimuli visually, by presenting stimuli quickly, and by using colors with low namability.

² Response times for correct trials were also examined in all perceptual control tasks. There was no difference between groups in the location WM task ($p = .45$), the face WM task ($p = .91$), or the color WM task (.21).

spatial locations that had been seen just 4 seconds earlier. There was trend towards a larger memory impairment when more information had to be retained, however the interaction of group and delay did not reach significance.

In Experiment 2, amnesics had poorer recognition memory for a single face. This finding extends those reported by Levy and Squire (2005) by showing large face memory deficits at delays as short as 4 s. Our stimuli had high inter-item similarity, potentially causing the larger memory impairment observed in our patients.

In Experiment 3, amnesics had poorer WM for three colors and performance did not change with a lengthier (8000 ms) delay. We have replicated the color results in a different group of MTL amnesics (Olson *et al.*, 2005a), adding validity to our findings.

There are a number of ways to interpret these findings, which we briefly discuss in the following paragraphs. First, one interpretation of these findings is that MTL amnesics have problems encoding visual stimuli into memory due to some sort of perceptual problem (Lee *et al.*, 2005). This idea seems unlikely given that MTL amnesics had intact perception of the stimuli used in the memory tasks - locations, faces, and colors (see Experiments 1, 2 and 3). However, there is the theoretical possibility that problems at encoding could take the form of *impoverished* encoding, leading to an unstable memory trace that quickly breaks down (Olson *et al.*, 2005-submitted).

A second possible explanation is that amnesic's visual WM deficits were due problems dealing with memory load. This hypothesis is implausible because in all experiments, memory load was lower than the upper bounds of visual WM capacity. Most people can accurately remember about 7 locations (Jiang *et al.*, 2000), 4 colors (Luck & Vogel, 1997), or 1.5 faces (Eng *et al.*, 2005-in press), suggesting that our results are not due to memory load.

The hypothesis that is most parsimonious and the most difficult to refute is that portions of the MTL, possibly the hippocampus, are critical for accurate visual WM, refuting the hypothesis that the MTL is only involved in long-term memory (Alvarez et al., 1994; Cave & Squire, 1992). Because the stimuli used in the three experiments were so different from one another, it must be assumed that the WM deficit is not particular to a class of stimuli but rather, is a general visual WM deficit. Our findings are consistent with recent neuroimaging findings that report activations of the hippocampus during visual WM tasks (Ranganath & D'Esposito, 2005). Some investigators interpreted these activations as establishment of a long-term memory trace for novel stimuli (Ranganath *et al.*, 2005-in press; Ranganath & D'Esposito, 2005; Schon *et al.*, 2004; Stern *et al.*, 2001) whereas others suggest that they reflected WM maintenance for certain classes of stimuli (Mitchell *et al.*, 2000a). It is difficult to give a strong interpretation to these findings given that the majority of fMRI studies have not reported MTL activations during WM tasks (Cohen *et al.*, 1997; Owen *et al.*, 1995; Postle *et al.*, 2000; Stern *et al.*, 2000). In addition, it must be noted that the inferential power of neuroimaging evidence is weak – it cannot tell us whether any given region is necessary for the cognitive process of interest.

Interpretive confusions have also plagued the amnesia literature with some investigators finding unexpected deficits in visual WM but interpreting such deficits as reflecting the beginning of long-term memory formation (Buffalo et al., 1998) or memory decline due to a change in context between study and test (Crane & Milner, 2005). The few studies that have reported visual WM deficits in amnesic patients have suffered from shortcomings such as failure to rule out perceptual deficits as a causative factor (Holdstock *et al.*, 1995; Owen et al., 1995), and grouping together patients with diencephalic and

MTL amnesia (Holdstock et al., 1995), thereby precluding inferences to be drawn about the relationship of anatomy to behavior.

Although the findings reported here were robust and consistent within our patient group, we believe that there may be instances in which WM is preserved in amnesic patients. First, it is likely that verbal WM does not rely on the MTL (Baddeley & Warrington, 1970; Cave & Squire, 1992; Wickelgren, 1968). Verbal information can be overtly rehearsed and various strategies enable one to easily remember verbal information. Also, verbal information tends to be semantically rich, allowing for the creation of a multi-faceted memory representation. In contrast, visual information is difficult to rehearse overtly and when the stimuli are unfamiliar, the representation is relatively sparse. Second, it is unlikely that all types of visual WM rely on the MTL. We have observed (Olson *et al.*, 2005b) that visual WM for common objects is intact in MTL amnesia, replicating findings from the developmental amnesic “Jon”, who has impaired visual long-term memory for visual topography but intact memory for objects (Spiers et al., 2001). This may be due to the fact that common objects possess a rich set of attributes, such as being familiar, verbalizable, highly differentiated, and semantically rich.

The Parietal Lobe and Visual WM

One of our patients, HT, had a small amount of left inferior parietal lobe damage (see Figure 2). Were her visual WM deficits due to this damage? Although the neural region most closely associated with spatial WM is the parietal lobe (Carlesimo *et al.*, 2001) there are several reasons why we do not believe HT’s parietal damage accounted for her poor WM performance. First, deficits in spatial WM are associated with right, not left parietal damage. Patients with contralesional neglect due to varied right parietal lobe

lesions fail to attend to the left side of space, and have recently been shown to have impaired spatial memory spans (Malhotra *et al.*, 2005; Pisella *et al.*, 2004).

Second, HT's parietal lesion was very small; patients with right parietal damage leading to spatial WM deficits tend to have very large lesions (Carlesimo *et al.*, 2001; Malhotra *et al.*, 2005; Pisella *et al.*, 2004). Third, HT had impaired location, face, and color WM, whereas previous reports suggest that parietal damage only affects spatial forms of WM (Pisella *et al.*, 2004). Last, the other two patients tested in these experiments did not have damage to the parietal lobe yet exhibited a similar pattern of WM deficits as HT.

Distinguishing Memory Systems

The results presented in this paper prompt consideration of whether visual WM can be clearly distinguished from visual long-term memory. The distinction between these entities is somewhat hazy (Crowder, 1982). Prior studies have shown that visual representations are tightly linked to information about orientation, and the structural relationship between object parts regardless of delay interval (Hollingworth, 2004). Moreover, visual representations are insensitive to information about absolute size and precise object contours, again, regardless of delay interval (Hollingworth, 2004). The most satisfying evidence for their independence comes from studies showing differences in capacity and a different group of studies showing differences in relevant neural structures. In regards to the former point, the capacity of VWM is quite small (Irwin, 1992; Luck & Vogel, 1997) the capacity of visual long-term memory is very large (Nickerson, 1968). However, the testing format of VWM requires great precision, perhaps at a cost to capacity, because one is required to compare two images that differ in some small way. In

comparison, tests of visual long-term memory typically use old/new recognition paradigms in which one can rely on familiarity, rather than direct comparison of stored visual memories.

In regards to the later point about differences in relevant neural structures, some studies have reported that MTL amnesics have intact visual WM (Alvarez et al., 1994; Cave & Squire, 1992; Levy & Squire, 2005), however interpretation of these findings has been clouded by ceiling effects and use of stimuli that encourage verbal encoding. Our findings show that MTL amnesics have impaired visual WM across many different stimulus types. The failure to find intact performance at short delays suggests that the distinction between visual short/working memory and visual long-term memory is less than clear.

Methods

Experiment 1

Participants. All participants were cooperative and attentive and had normal or corrected-to-normal visual acuity. All participants signed an informed consent form prior to taking part in the experiment. Control participants were seven older healthy adults (3 males, 4 females, 45-71 yrs, $M=60$ yrs) with an average of 13 years of education. Average verbal IQ as measured by the Wechsler Adult Intelligence Scale-third edition (Wechsler, 1997a) was 108.

The lesion group consisted of three patients with bilateral medial temporal lobe damage (1 males, 2 females, 62-68 yrs, $M=65$ years; see Figure 2) who had an average of 12 years of education. Average verbal IQ was 92. General Memory score on the WMS-third edition (Wechsler, 1997b) was 60 and the Visual Delayed Memory score was 62.

There was no difference between the MTL group and their control group in terms of age ($p=.34$), education ($p=.27$), or verbal IQ ($p=.065$). Detailed information about each patient is listed below.

Patient MS

Patient MS (age 62) has bilateral medial temporal lobe damage as a result of herpes encephalitis in 1999. Damage extends into the amygdala, perirhinal, and hippocampal cortex on the left, entorhinal and hippocampal cortex on the right, as assessed by MRI. Damage on the left extends in posterior temporal regions. MS's chief complaint is anomia, which has steadily improved over time, but is still impaired. When shown Snodgrass line drawings, she only named 16/65 correct.

Patient HT

Patient HT (age 64) has focal bilateral hippocampal damage as evidenced by hypertensities in the hippocampus on T2 weighted MR scans (left greater than right), as well as hyperintensity in the left parietal lobe. Damage was caused in the setting of a basilar meningitis and CNS vasculitis. Her family reports that her behavior is unchanged from the past except for a radical decline in her memory. She self reports that she can no longer read novels or watch television because she cannot follow the story line. In addition, she sometimes gets confused when having a conversation, due to an inability to remember the topic of conversation. She has difficulty navigating and is not allowed to drive. Because her MRI showed a left inferior parietal hyperintensity, her naming abilities were assessed with the Boston Naming Test which consists of the presentation of line drawings that vary from high to low frequency. No deficit was found (7/8). Her reading was assessed by requiring her to read aloud 16 printed words. No deficit was found (15/16).

Patient CT

Patient CT (age 68) has MTL damage as a result of encephalitis in 2001. His MR scans show damage to the left anterior hippocampus and portions of the entorhinal cortex and more limited damage to the right anterior hippocampus. He self reports that he can no longer navigate and gets lost in his own neighborhood. His wife drives him to his neurology appointments. His naming abilities are intact as shown by his Boston naming score of 58/60. Although he is officially retired, he continues to work part time as a skilled cabinetmaker. This ability has not declined since his neurological insult, but he now must write everything down, being unable to commit details about style and size to memory.

Equipment

Participants were tested individually on either a laptop computer or a desktop computer. They sat at an unrestricted viewing distance of about 57cm, at which distance 1cm corresponds to 1° viewing angle. The experiment was programmed in MATLAB with Psychtoolbox (Brainard, 1997) for Macintosh.

Materials

On each memory image several green (RGB 0 255 0) squares (1.1°x 1.1°) were presented on a uniformly gray background (RGB 127). The items were presented at randomly selected locations in a 10 x 10 invisible matrix that subtended 17.7° x 17.7°. The stimuli were designed so that squares could not touch one another.

Procedure

Each trial started with a memory image containing $N - 3$ or 6 - filled locations denoted by green squares lasting 1000 ms (Figure 1a). After a blank interval of 4000 ms, a probe array containing $N-1$ green squares was presented. The task was to recall which locations had been filled on the memory image and then decide which filled location was missing

from the array on the probe image. Responses were made by unspeeded mouse-click on the missing location. The probe display was cleared and accuracy feedback in the form of a high-pitched tone (correct responses) or nothing (incorrect responses) was provided immediately after the mouse click was made. Responses were coded as correct if the mouse-click was within 5 mm of the outside edges of the green square (Dale, 1973; Keefe *et al.*, 1997). The next trial commenced after a 500 ms interval. The testing session began with 10 practice trials and was followed by 50 test trials, 25 of set size 3, 25 of set size 6.

Perceptual Control Task

The computer screen was divided into two halves and a memory image appeared on the left half, and a probe image appeared on the right half. Images were the same as used in the memory task, but smaller. The task was to look at the two images, and to make an unspeeded mouse-click on the missing square in the right image. The entry of the response cleared the screen, auditory feedback was given, and the next trial commenced after a 500 ms interval. There were 14 trials.

Experiment 2

Materials

Each face was presented on a uniformly black background at central fixation. The faces were drawn from a pool of 200 forward-facing male and female faces provided by the Max-Planck Institute (<http://faces.kyb.tuebingen.mpg.de/index.php>). Faces were standardized to be of similar size, age, and race. Faces were Caucasian, in color, had neutral expressions, and were devoid of hair, glasses, or other non-face features. Each face subtended 3.8° of visual angle (37.5 mm).

Procedure

Each trial started with an orienting cue consisting of the words "Get Ready to Remember" for 500 ms in the middle of the screen followed by a blank screen for 500 ms (see Figure 1b). This was followed by a memory image containing one face, for 1000 ms, a retention interval consisting of a blank screen for 4000 ms, and then a probe image containing one face, lasting until a response was made. One half of the time the face matched the face from the memory image (=match trial), the other half of the time the face was different from the face on the memory image (=mismatch trial). Trial types were randomly interleaved. Responses were made by unspeeeded keypress. Immediately after the response was made, the probe image was cleared and accuracy feedback was provided. The next trial commenced after a 500 ms interval. The testing session began with 12 practice trials and was followed by 96 trials.

Perceptual Control Task

Two faces, drawn from a reserved portion of the face database that was tested in the memory task, were presented side by side and the task was simply to indicate by unspeeeded keypress whether the faces were the same or different. Response entry cleared the screen and the next trial commenced after a 500 ms interval. There were 14 trials.

Statistical Analysis.

Hit rates (responding "yes" on a match trial) and false alarm rates (responding "yes" when the item had not been on a match trial) were used to calculate corrected recognition (hits-false alarms) in Experiments 2 and 3.

Experiment 3

Materials

The stimuli consisted of three color patches presented on a gray background separated into quadrants by black crosshairs (see Figure 1c). Colors were defined using the RGB system. The stimulus colors tested were: orange red [255 90 0], peach [238 198 0], chartreuse [150 255 0], aqua [71 177 153], cobalt[0 114 255], indigo[130 0 201], magenta [255 0 255], and burgundy[171 11 67]. Colors were pilot tested to insure difficulty of applying verbal labels. Stimulus size was 1.5cm x 1.5 cm. Stimuli were randomly located in an invisible 8 X 8 matrix with the constraint that each item occupy a unique quadrant. The memory image subtended 15° (15cm x 15cm). The crosshairs remained on the screen between trials and stimulus presentations to serve as a reference frame.

Procedure

Each trial started with an orienting cue consisting of the words "Get Ready to Remember" for 500 ms in the middle of the screen followed by a blank screen for 500 ms. This was followed by the memory image containing three colors, that lasted for 1000 ms. This was followed by a blank retention interval of 4000 or 8000 ms, and then a probe image containing three colors, one of which was cued by a surround box, that lasted until a response was made. The task was to report by keypress whether the cued color was the same as the color that had occupied that location on the memory image. Responses were made by unspeeded keypress. The probe image was cleared and accuracy feedback was provided immediately after the response was made. The next trial commenced after a 500 ms interval. The testing session began with 12 practice trials and was followed by 72 test trials.

Perceptual Control Task

Two color memory images, each 5cm x 5cm in size, were presented side by side and the task was simply to indicate by unspeeded keypress whether all colors were the same in both memory images, or one was different. Response entry cleared the screen and the next trial commenced after a 500 ms interval. There were 14 trials.

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Figure Legends

Figure 1. A schematic diagram of the tasks used in (a) Experiment 1; (b) Experiment 2; and (c) Experiment 3. In the actual experiment, the stimuli used in Experiments 1 and 3 were colored.

Figure 2. Axial MRI scans from the three patients, MS, HT, and CT, shown in radiological convention (e.g. left on the right). Images for MS and HT are fluid-attenuated inversion recovery (FLAIR) and for CT are T2 weighted.

Figure 3. Results from the location WM task (Experiment 1). Spatial displacement (error) in mm as a function of set size. Error bars represent standard error of the mean.

Figure 4. Results from the face WM task (Experiment 2). Corrected accuracy (hit rate-false alarm rate) as a function of epoch. Error bars represent standard error of the mean.

Figure 5. Results from the color WM task (Experiment 3). Corrected accuracy (hit rate-false alarm rate) as a function of epoch. Error bars represent standard error of the mean.

Figure 1

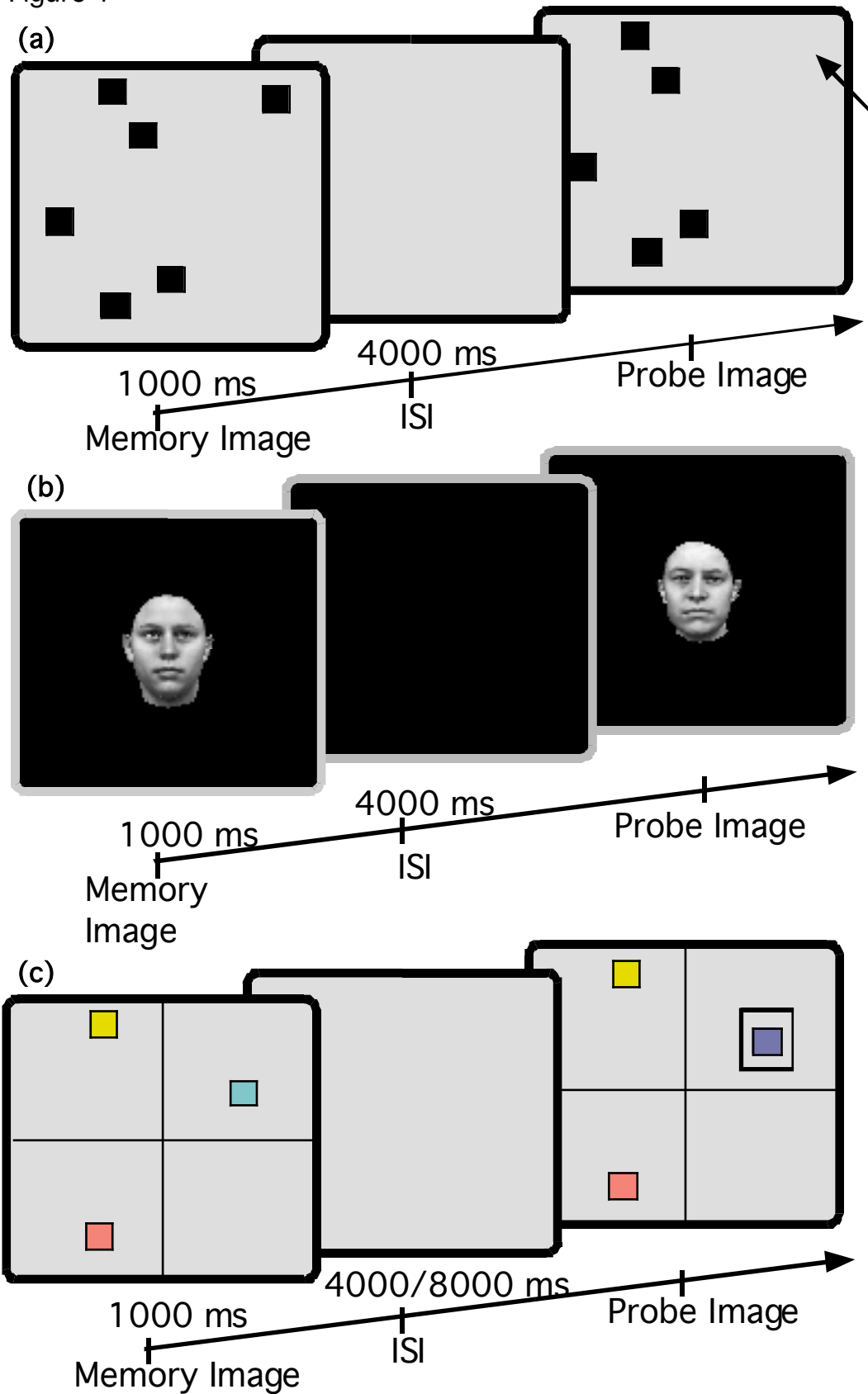


Figure 2

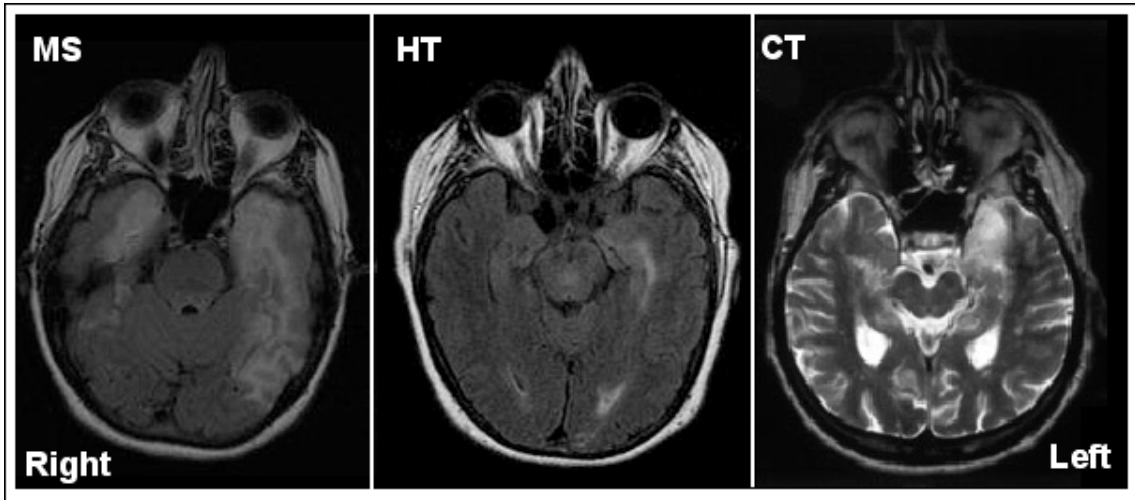


Figure. 3

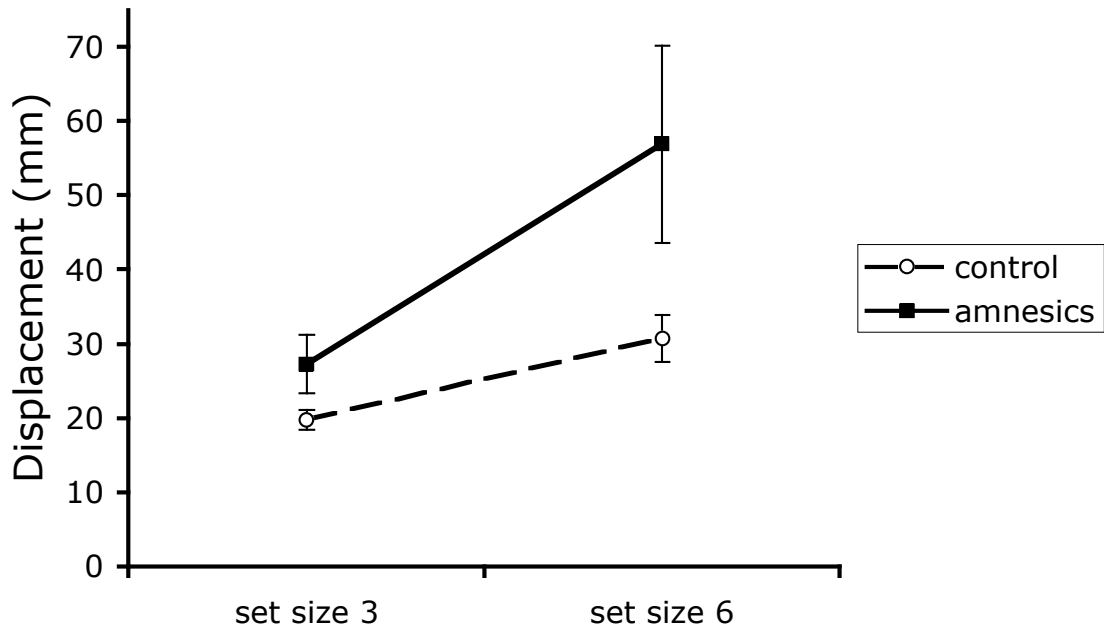


Figure 4.

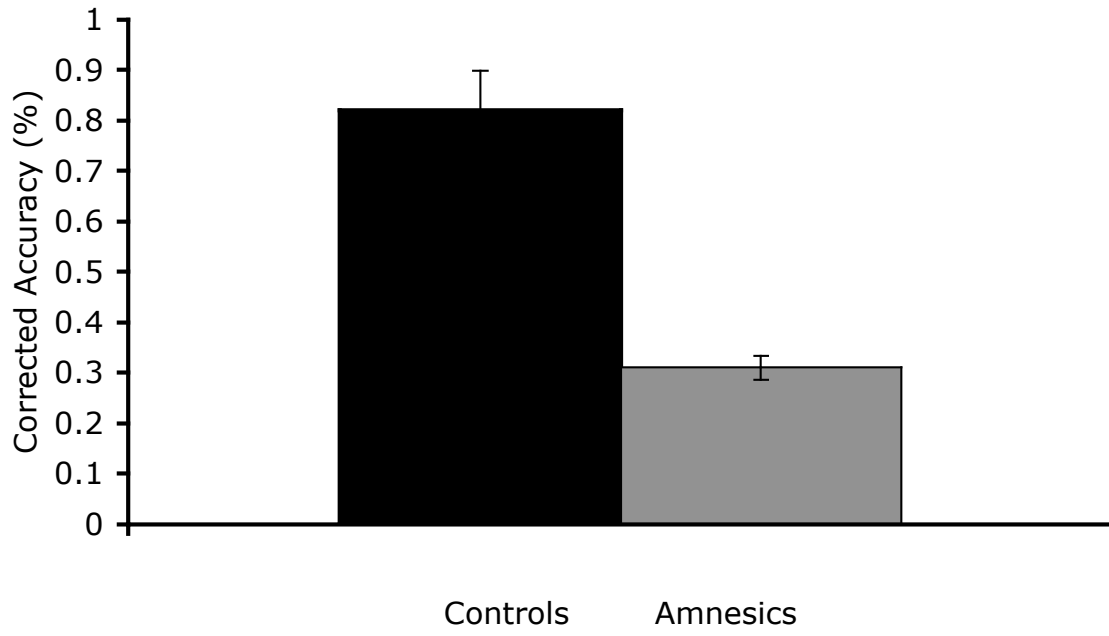


Figure 5.

