



Preserved capacity for learning statistical regularities and directing selective attention after hippocampal lesions

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Prior knowledge about the probabilistic structure of visual environments is necessary to resolve ambiguous information about objects in the world. Expectations based on stimulus regularities exert a powerful influence on human perception and decision making by improving the efficiency of information processing. Another type of prior knowledge, termed top-down attention, can also improve perceptual performance by facilitating the selective processing of relevant over irrelevant information. While much is known about attention, the mechanisms that support expectations about statistical regularities are not well-understood. The hippocampus has been implicated as a key structure involved in or perhaps necessary for the learning of statistical regularities, consistent with its role in various kinds of learning and memory. Here, we tested this hypothesis using a motion discrimination task in which we manipulated the most likely direction of motion, the degree of attention afforded to the relevant stimulus, and the amount of available sensory evidence. We tested memory-impaired patients with bilateral damage to the hippocampus and compared their performance with controls. Despite a modest slowing in response initiation across all task conditions, patients performed similar to controls. Like controls, patients exhibited a tendency to respond faster and more accurately when the motion direction was more probable, the stimulus was better attended, and more sensory evidence was available. Together, these findings demonstrate a robust, hippocampus-independent capacity for learning statistical regularities in the sensory environment in order to improve information processing.

expectation | memory | hippocampus

Visual input provides inherently ambiguous information about objects in the world (1). Prior knowledge about the probabilistic structure of the world plays a critical role in resolving this ambiguity (2). Thus, expectations about statistical regularities can improve the efficiency of decision making (3–16). For example, we learn from past experience that certain objects are more likely to be seen in particular contexts. Thus, when presented with an image of a gym, people are better at recognizing and processing information about a treadmill than a piano (17, 18).

A second factor that is based on prior knowledge, termed top-down attention, can also improve perceptual performance by facilitating the processing of information that is immediately relevant in the context of current behavioral goals (19–21). Attention sharpens the quality of relevant information by increasing the responsiveness of neurons in early visual cortex to task-relevant signals (22–24). Thus, when looking for your car in a parking lot, knowledge about its color, shape, and size can improve search by selectively facilitating the processing of potentially relevant target features. Critically, these 2 types of prior knowledge (expectation and top-down attention) are different, because expectations about what stimuli will be encountered in a given context can be entirely

independent of what stimuli are attended based on behavioral relevance.

While much is known about attention, the process by which expectation about statistical regularities is acquired and used to guide behavior is not well-understood. The hippocampus has been implicated as a key structure involved in or perhaps necessary for the learning of statistical regularities (25, 26). In one study, controls were faster on a visual search task when search displays were repeated than when they were novel, but amnesic patients did not exhibit this advantage (25). There is some ambiguity about what damage was responsible for this impairment, because MRI scans were available for only 2 of the 4 patients tested and these indicated damage extending well beyond the hippocampus. In a subsequent study (27), patients with hippocampal damage confirmed by MRI performed similar to controls, that is, patients, like controls, searched repeated displays faster than novel displays. An impairment was observed only in a patient with damage extending beyond the hippocampus to include the parahippocampal gyrus and lateral temporal cortex.

In another study (26), a patient with large lesions of the medial temporal lobe viewed a long sequence of stimuli that contained a repeating pattern of 12 items. Unlike controls, the patient failed to learn the pattern. However, knowledge was assessed by asking

Significance

The hippocampus is important for many kinds of learning and memory. We explored the role of the hippocampus in the learning of statistical regularities. We administered a motion discrimination task where expectation about stimulus regularities, the degree of attention afforded to the relevant stimulus, and the amount of available sensory information were manipulated. Although modestly slower overall, patients with bilateral damage to the hippocampus performed similar to controls, exhibiting a normal tendency to respond faster and more accurately when the motion direction was more probable, when the stimulus was better attended, and when more sensory evidence was present. These findings show that the ability to acquire expectations based on regularities of a sensory environment can be independent of the hippocampus.

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participants to explicitly report or recognize the repeating pattern. These measures are unlikely to be representative of the patient's knowledge, as memory-impaired patients can exhibit knowledge about the regularities in sequences indirectly through performance, despite an inability to verbally report declarative knowledge about the sequence (28). In the same way, patients can successfully acquire skills or habits even when they are unable to express knowledge about the task itself (29–31). Notably, in a serial reaction time task, hippocampal patients and controls learned a 12-item sequence of 4 button presses guided by visual cues (28). Reaction time improved as participants practiced the sequence and came to anticipate the order in which the cues appeared. Critically, both groups markedly slowed their reaction times when the sequence was unexpectedly changed, thereby demonstrating that they had learned the sequence. Nevertheless, the patients were unable to verbally report the sequence or to recognize it. These considerations point out the utility of indirect, performance-based measures to assess knowledge about statistical regularities and raise doubts about the importance of the hippocampus in acquiring such information.

The present study examined the contribution of the hippocampus to the learning of statistical regularities more directly by devising a motion discrimination task in which expectation was manipulated by presenting one (expected) motion direction more frequently than other (unexpected) directions. Four memory-impaired patients with bilateral damage to the hippocampus, as well as controls, reported the direction of motion by moving a joystick from the starting point to an end point along a trajectory from 0 to 360° (Fig. 1). We also included 2 additional conditions: (i) a manipulation of the amount of sensory information (high versus low motion coherence) available in each stimulus display, and (ii) a manipulation of top-down attention (focused versus divided). Manipulating the amount of sensory information allowed us to parametrically assess interactions between the strength of sensory signals with top-down attention and expectation. Notably, sensory and attentional processes are thought to be independent of hippocampal function on the basis of findings from patients such as H.M. and E.P. (25–28). Accordingly, the manipulations of sensory information and attention serve as control or baseline conditions against which to evaluate the ability of patients to form and use expectations about statistical regularities.

Results

Response Trajectories. The response trajectory indicated how far the joystick had moved from the center at each time point (0 to 1,500 ms). The coherence level of the motion displays (high/low coherence) affected controls and patients similarly (Fig. 2*A*). For controls, the trajectory amplitudes were different from 567 to 1,408 ms after stimulus onset (high > low coherence). For patients, the trajectory amplitudes were different from 633 to 1,225 ms after stimulus onset (high > low coherence) (all resampled $P < 0.05$).

Manipulations of attention (focused/divided) also affected controls and patients similarly (Fig. 2*B*). For controls, the trajectory amplitudes were different from 550 to 1,392 ms after stimulus onset (focused > divided). For patients, the trajectory amplitudes were different from 600 to 1,492 ms after stimulus onset (focused > divided) (all resampled $P < 0.05$).

Expectation (expected/unexpected) also affected controls and patients similarly (Fig. 2*C*). For controls, the trajectory amplitudes were different from 508 to 892 ms after stimulus onset (expected > unexpected) and also from 1,400 to 1,500 ms after stimulus onset (unexpected > expected). This effect is not visually remarkable in Fig. 2*C*, but is clear in Fig. 2*D*. For patients, the trajectory amplitudes were different from 567 to 1,017 ms after stimulus onset (expected > unexpected) and also from 1,258 to 1,500 ms after stimulus onset (unexpected > expected). Fig. 2*D* summarizes the effects of coherence level, attention, and expectation. Fig. 2*E* shows the P values for each condition and

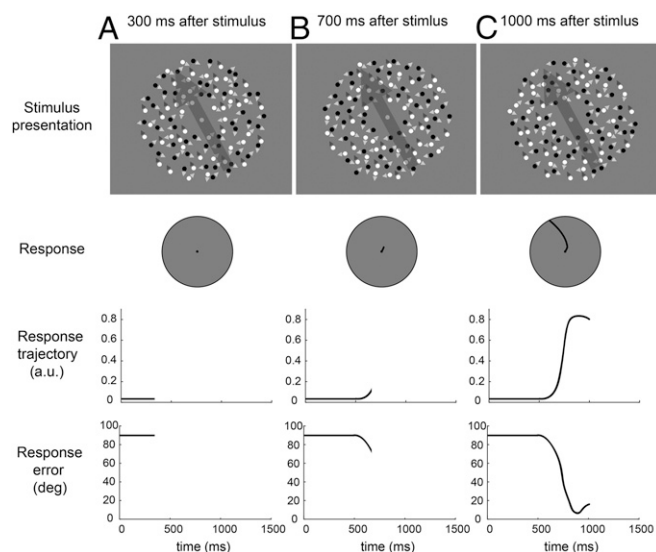


Fig. 1. Sample trial. A trial began with an attention cue (1,000 to 1,500 ms) to indicate the color of the dots that would represent coherent motion. A white (black) attention cue indicated that coherent motion would be represented with white (black) dots. A blue attention cue indicated that coherent motion would be represented with either white or black dots, that is, the participant had to discern which color of dots was in coherent motion. (A) At 300 ms after stimulus onset (motion direction 112° in this case, as indicated by the arrow), the participant has not yet begun a response, and the black dot represents the stationary joystick. The response trajectory, which is the distance that the joystick has moved from the center, remains close to 0, and the response error is approximately at chance (90°). (B) At 700 ms after stimulus onset, the participant has accumulated some information about the direction of coherent motion and begun a response, trying to match the movement of the joystick to the direction of motion. The response error shows the difference between the direction of the participant's response and the target motion direction at each time point. (C) At 1,000 ms after stimulus onset, the participant has moved the joystick its maximal distance. The response trajectory reaches its maximum at this time, and the response error is now close to 0.

at each time point (0 to 1,500 ms) (all resampled $P < 0.05$). There were no interactions between coherence levels, attention, and expectation on response trajectories for either controls or patients.

Patients performed similar to controls across all 3 manipulations of coherence level, attention, and expectation. Each patient performed within the 95% confidence intervals of the control group in all conditions (*SI Appendix*). Note that the onset of these effects was delayed in patients compared with controls (coherence level: 567 ms [controls] vs. 633 ms after stimulus onset [patients]; attention: 550 ms [controls] vs. 600 ms [patients]; expectation: 508 ms [controls] vs. 567 ms [patients]; all resampled $P < 0.05$). As this effect was similar across manipulations of bottom-up sensory information and top-down factors like attention and expectation, this slowing likely reflects a modest impairment in the ability of patients to exploit available perceptual information in the service of decision-making tasks (27, 28, 32).

Response Errors. Response errors were computed as the absolute difference at each time point between the participant's response angle and the calibrated angle for that participant. The magnitude of the response errors, before and after the onset of the joystick movement, indexed the accuracy of the direction judgment of participants.

The coherence level of the presented motion directions (high/low coherence) affected controls and patients similarly (Fig. 3*A*). For controls, the magnitude of the response errors was different

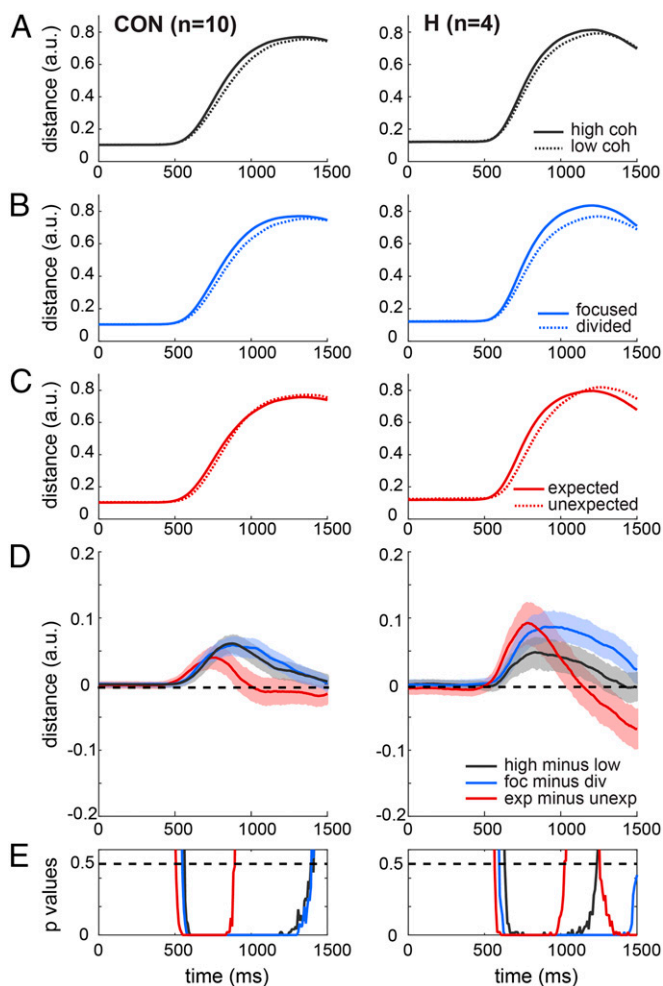


Fig. 2. Response trajectories. Response trajectories for controls and patients with hippocampal lesions were plotted from the onset of coherent motion (0 ms) to 1,500 ms after onset. (A–C) Response trajectories were plotted (A) as a function of coherence level (high/low), (B) as a function of attention (focused/divided), and (C) as a function of expectation (expected/unexpected). (D and E) Differences in response trajectories for each manipulation condition were plotted together with the associated *P* values. From 567 to 1,408 ms in controls, and from 633 to 1,225 ms in patients (A), the joystick had moved farther when coherent motion was presented at a high coherence than at a low level (resampled $P < 0.05$). From 550 to 1,392 ms in controls, and from 600 to 1,492 ms in patients (B), the joystick had moved farther when attention was focused than when attention was divided (resampled $P < 0.05$). From 508 to 892 ms in controls, and from 567 to 1,017 ms in patients (C), the joystick had moved farther when coherent motion was presented in the expected direction than in the unexpected direction (resampled $P < 0.05$). In addition, from 1,400 to 1,500 ms in controls, and from 1,258 to 1,500 ms in patients (C), the joystick had moved farther when coherent motion was presented in the unexpected direction than in the expected direction (resampled $P < 0.05$). For E, the legend is the same as in D. Error bars for each of the 3 measures indicate 95% CIs computed by resampling the data distribution.

from 642 to 1,100 ms after stimulus onset (high < low coherence). For patients, the magnitude of the response errors was different from 733 to 1,050 ms after stimulus onset (high < low coherence) (all resampled $P < 0.05$).

Attention (focused/divided) also affected controls and patients similarly (Fig. 3B). For controls, the magnitude of the response errors was different from 567 to 1,133 ms after stimulus onset (focused < divided). For patients, the magnitude of the response errors was different from 775 to 817 ms after stimulus onset (focused < divided) (all resampled $P < 0.05$).

Expectation (expected/unexpected) also affected controls and patients similarly (Fig. 3C). For controls, the magnitude of the response errors was different from 0 to 708 ms after stimulus onset (expected < unexpected). For patients, the magnitude of the response errors was different from 0 to 1,067 ms after stimulus onset (expected < unexpected) (all resampled $P < 0.05$). Fig. 3D summarizes the effects of coherence level, attention, and expectation. Fig. 3E shows the *P* values for each condition and at each time point (0 to 1,500 ms). There were no interactions between coherence levels, attention, and expectation on response errors for either controls or patients. Each patient performed within the 95% confidence intervals of the control group in all conditions (SI Appendix).

Discussion

We examined the contribution of the hippocampus to the ability to learn statistical regularities by devising a motion discrimination task where expectation about motion direction was manipulated such that one (expected) direction was presented more frequently than other (unexpected) directions. We also asked if patients with lesions to the hippocampus would benefit as much as controls from the effects of focused versus divided attention and from the effects of strong versus weak sensory evidence. Despite a modest slowing in response initiation across all task conditions, patients performed similar to controls. Both controls and patients exhibited a similar benefit of expectation on response accuracy and speed beginning immediately after stimulus onset (Figs. 2C and 3C), both groups responded more quickly and more accurately when attending to 1 color of dots versus 2 colors (Figs. 2B and 3B), and both groups responded more quickly and more accurately when the sensory evidence was strong (high coherence) than when it was weak (low coherence) (Figs. 2A and 3A). Together, these findings indicate that the ability to learn statistical regularities, selectively attend to behaviorally relevant stimuli, and perform better when given stronger sensory evidence is intact after bilateral hippocampal lesions.

The present study used a continuous decision task, such that performance could be assessed at all time points from stimulus onset to response offset. Participants reported the direction of motion by moving a flight simulator joystick along a path (0 to 360°) to match the perceived direction of moving dots. Knowledge about the statistical regularities of motion direction was indirectly assessed by measuring how far the joystick had moved and how accurate the response was at each time point. These indirect, performance-based measures were used because hippocampal patients have been shown to acquire skills and habits even when they do not have explicit knowledge about the task itself (28), and even when they are unaware that they have been tested before (29–31).

Expectation about statistical regularities improves information processing and behavior in a variety of perceptual tasks (2, 14–16, 33–35). Past work suggested that the hippocampus might be critical in the learning of statistical regularities (25, 36) in light of its importance for many forms of learning and memory. In our study, however, patients successfully learned about statistical regularities, and they were able to exploit expectations as well as controls. Our results are in line with an earlier study that tested hippocampal patients in a serial reaction time task. In that study, participants learned a sequence of button presses guided by visual cues (28). Reaction time for both controls and patients improved as they practiced the sequence and successfully learned the order in which the lights would appear. Like controls, patients slowed their reaction times when the sequence of lights unexpectedly changed. Despite this evidence for implicit knowledge about the learned sequence, the patients were unable to verbally report the sequence or to recognize it among 4 choices. A similar finding was reported in an earlier study of statistical learning in which a patient with large medial temporal lobe lesions attempted to learn a repeating pattern of 12 items (26).

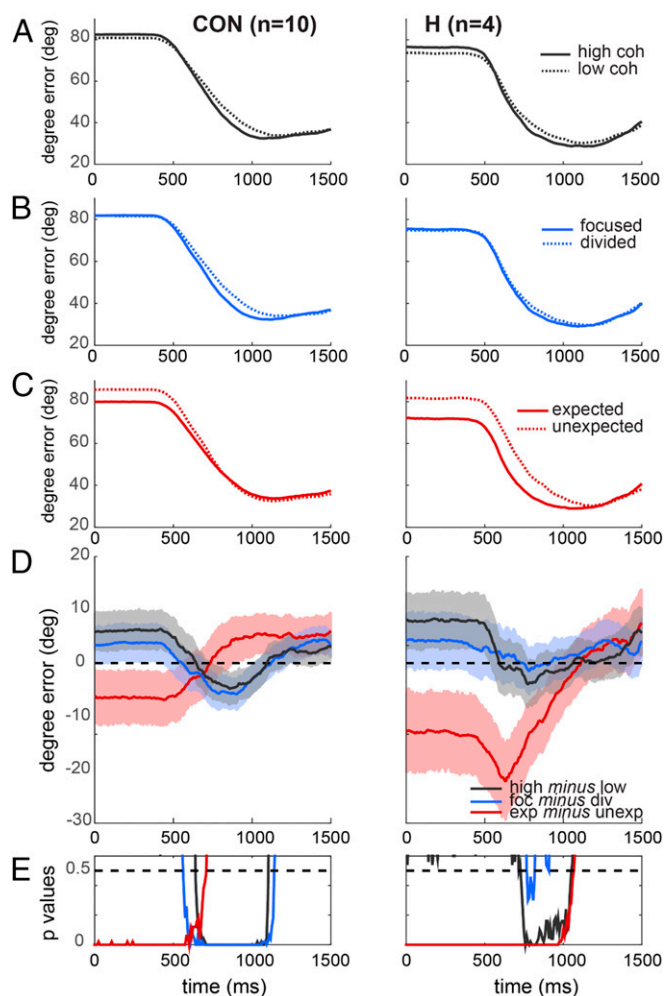


Fig. 3. Response errors. Response errors for controls and patients with hippocampal lesions were plotted from the onset of coherent motion (0 ms) to 1,500 ms after onset. (A–C) Response errors were plotted (A) as a function of coherence level (high/low), (B) as a function of attention (focused/divided), and (C) as a function of expectation (expected/unexpected). (D and E) Differences in response trajectories for each manipulation condition were plotted together with the associated *P* values. From 642 to 1,100 ms in controls, and from 733 to 1,050 ms in patients (A), response errors were lower when coherent motion was presented at a high coherence than at a low level (resampled $P < 0.05$). From 567 to 1,133 ms in controls, and from 775 to 817 ms in patients (B), response errors were lower when attention was focused than when attention was divided (resampled $P < 0.05$). (C) Expectation reduced baseline response errors (i.e., at the onset of coherent motion; 0 ms), and this effect lasted until 708 and 1,067 ms after stimulus onset in controls and patients, respectively (resampled $P < 0.05$). For E, the legend is the same as in D. Error bars for each of the 3 measures indicate 95% CIs computed by resampling the data distribution.

As in Reber and Squire (28), this patient also failed to exhibit knowledge of the sequence when asked for an explicit report of the repeating sequence or when asked to recognize it. However, the patient was not tested using indirect, performance-based measures that might have revealed implicit knowledge about the sequence.

One way in which our task differed from previous tasks is in the nature of the information needed to be learned and used to support performance. To benefit from statistical learning in our task, participants had to form knowledge about the direction of motion that had the highest probability of being presented in each test block. It is possible that the statistical learning of other kinds of information (such as spatial locations) might yield different results.

With the current task, we cannot determine if the effects of expectation on response error reflect response bias or changes in perceptual sensitivity or both. However, recent work has demonstrated that response bias (i.e., expectation about motor responses) affects information processing in the same manner as expectation about stimulus features such as stimulus color and orientation (34, 35). In addition, there is an effect of response error at 0 ms (i.e., stimulus onset), consistent with an important role for response bias. Thus, we argue that the effects on response errors are primarily driven by changes in response bias that occurred due to learned expectations about the motor responses associated with each of the expected coherent motion directions.

In the present study, patients also benefited as much as controls from manipulations of attention and the amount of available sensory evidence. These findings are consistent with a sizeable literature showing that patients with hippocampal lesions perform well on tests of intelligence and perceptual function (37–41). That said, previous work has not specifically examined the importance of the hippocampus for the top-down deployments of selective attention. Thus, the intact performance reported here, though not surprising, demonstrates directly that the hippocampus is not necessary to exploit attentional cues in order to determine behavioral relevance.

In summary, we evaluated statistical learning, attention, and processing of sensory evidence in memory-impaired patients with circumscribed hippocampal lesions. Patients and controls performed similarly in all respects. Thus, patients exhibited a normal tendency to perform faster and more accurately when the stimulus was probable, behaviorally relevant, and provided stronger sensory evidence. These findings demonstrate a robust capacity for acquiring expectations about statistical regularities in the sensory environment that can operate independent of the hippocampus.

Methods

Participants. Four memory-impaired patients participated with bilateral lesions thought to be limited to the hippocampus (CA fields, dentate gyrus, and subicular complex) (Table 1). Patients D.A. and G.W. became amnesic in 2011 and 2001, respectively, following a drug overdose and associated respiratory failure. K.E. became amnesic in 2004 after an episode of ischemia associated with kidney failure and toxic shock syndrome. L.J. (the only female) became amnesic during a 6-mo period in 1988 with no known precipitating event. Her memory impairment has been stable since that time.

For the 4 patients, the average score per passage for delayed recall (30 min) of 2 short prose passages was 1.0 segment (25 segments per passage). The average score for delayed recall (10 min) of a complex diagram was 5.4 (maximum score 36). Paired-associate learning of 10 unrelated noun–noun pairs summed across each of 3 successive trials was 3.8 pairs (30 pairs total) (Table 2). On these same tests, 11 controls scored 20.2 for the prose passages, 18.3 for the diagram, and 24.1 for paired-associate learning (42).

Estimates of medial temporal lobe (MTL) damage were based on quantitative analysis of magnetic resonance (MR) images from 19 age-matched, healthy males for K.E. and G.W., 11 age-matched, healthy females for patient L.J. (43), and 8 young healthy males for D.A.; patients D.A., K.E., L.J., and G.W. have an average bilateral reduction in hippocampal volume of 35, 49, 46, and 48%, respectively (all values are at least 2.9 SDs from the control mean). On the basis of 2 patients (L.M. and W.H.) with similar bilateral volume loss in the hippocampus for whom detailed postmortem neurohistological information was obtained (44), the degree of volume loss in these four patients may reflect nearly complete loss of hippocampal neurons. That is, patients L.M. and W.H. had a nearly complete loss of hippocampal neurons, despite exhibiting considerable sparing of hippocampal volume as measured by MRI. Apparently, neuronal death need not lead to disappearance of all hippocampal tissue, perhaps because the tissue can be supported to some extent by glia and white matter.

The volume of the parahippocampal gyrus (temporopolar, perirhinal, entorhinal, and parahippocampal cortices) is reduced by -5 , 11 , -17 , and 10% , respectively (all values within 2 SDs of the control mean). Minus values indicate volumes that were larger for a patient than for controls. These values are based on published guidelines for identifying the boundaries of the parahippocampal gyrus (45, 46). Eight coronal magnetic resonance

Table 1. Characteristics of memory-impaired patients

Patient	Age, y	Education, y	WAIS-III IQ	WMS-R				
				Attention	Verbal	Visual	General	Delay
D.A.	34	12	95	104	90	91	90	56
K.E.	76	13.5	108	114	64	84	72	55
L.J.	81	12	101	105	83	60	69	<50
G.W.	58	12	108	105	65	86	70	<50

WAIS-III, Wechsler Adult Intelligence Scale III; WMS-R, Wechsler Memory Scale Revised. The WMS-R does not provide numerical scores for individuals who score <50. The IQ score for D.A. is from the WAIS-IV.

images from each patient, together with detailed descriptions of the MTL lesions, can be found elsewhere (47).

Ten healthy controls (3 female) also participated (mean age 64.9 ± 13.5 y; mean education 14.3 ± 1.8 y). All procedures were approved by the Institutional Review Board at the University of California, San Diego, and both patients and controls gave written informed consent prior to participation.

Stimuli. In each of 2 ~1-h test sessions, participants completed a block of calibration trials ($n = 60$ trials), a block of practice trials ($n = 104$ trials), and 5 test blocks ($n = 104$ trials for each block).

For the calibration trials, stimuli consisted of 400 black dots (diameter 0.18°) displayed in an annulus (outer diameter 22° ; inner diameter 2.4°) on a dark gray background (luminous intensity 42.68 ± 2.20 cd/m²; Fig. 1). Black dots within the annulus were flickered at 33 Hz for the duration of the trial, and each dot was randomly replotted on each frame. On each trial, 100% of the dots (i.e., 100% coherence) were coherently moved in one of the 5 possible motion directions (46 to 334° with 72° increments). Dot stimuli moved at a speed of 100 pixels per ms. Participants were instructed to report the motion direction of these moving dots via a USB-compatible flight simulator joystick. The purpose of the calibration trials was to estimate how each participant represented each motion direction. These estimates were used to compute performance accuracy on the test trials.

For the practice and test trials, stimuli consisted of 200 black dots and 200 white dots (diameter 0.18°) displayed in an annulus, as in the calibration trials, but surrounding an attention cue of either black, white, or blue. Black and white dots within the annulus were flickered at 33 Hz for the duration of the trial, and each dot was randomly replotted on each frame. During coherent motion, either 50% (low coherence) or 70% (high coherence) of the black (or white) dots was randomly selected on each frame to be displaced in one of 5 possible motion directions (46 to 334° with 72° increments), while the remaining dots were assigned one of 5 other motion directions. Dot stimuli moved at a speed of 100 pixels per ms. Participants were instructed to report the motion direction of the moving dots via a USB-compatible 360° flight simulator joystick.

Stimuli were presented on a PC with Windows XP using MATLAB (MathWorks) and the Psychophysics Toolbox [version 3.0.8 (48, 49)]. Participants were seated 60 cm from the CRT monitor running at 100 Hz with a gray background of 42.68 ± 2.20 cd/m².

Procedure. Participants performed a version of the random dot motion task (50–52), such that the amount of sensory evidence (coherence levels), selective attention, and expectation about target direction could be manipulated. Participants completed 2 test sessions, each of which consisted of calibration trials, practice trials, and 5 blocks of test trials as described above. Each test trial began with a display consisting of an attention cue, either black, white, or blue. A black or white cue informed participants to monitor either the black or white dots (focused attention), and the blue cue informed participants to monitor both black and white dots (divided attention) to determine which color of dots displayed coherent motion. After 1,000 to 1,500 ms, black and white moving dots were presented for 2,000 ms, such that a proportion, either 50% (low coherence) or 70% (high coherence) of either black or white dots, formed coherent motion in one of the 5 possible directions. The remaining dots were randomly assigned to the other 4 directions. Note that the attention cue was always valid such that on focused-attention trials the coherent motion was represented by black dots on half the trials and by white dots on half the trials. For each test block of 104 trials, half of the test trials were focused-attention trials and the other half were divided-attention trials, yielding a total of 520 trials for focused- and divided-attention conditions for each participant in each of the 2 test sessions. Presentation of the moving dots was followed by a 500- to 800-ms blank intertrial interval (ITI). For each test block, expectation about motion

direction was manipulated such that one (expected) direction (out of 5 possible directions) was presented on 69.2% of trials (72 trials per block), whereas the other (unexpected) directions were presented equally on the remaining 30.8% of trials (32 trials per block). The expected motion direction differed from one test block to another such that each of the 5 possible motion directions was assigned as the expected direction in just one block per session. Participants indicated the target motion direction by moving the flight simulator joystick its maximal distance in a direction matching the coherent motion. After making a response, participants returned the joystick to the center in preparation for the next trial. Responses were considered valid when they occurred in the interval between stimulus onset and ITI offset. In summary, each participant was given 1,040 trials. All 3 factors of interest (attention, expectation, and coherence levels) were manipulated orthogonally such that each participant was given a total of 520 focused-attention trials (260 of which were low-coherence trials and the other 260 high-coherence trials), 520 divided-attention trials (260 of which were low-coherence trials and the other 260 high-coherence trials), 720 expected trials, and 320 unexpected trials.

To familiarize participants with the task and the joystick, practice trials were given at the beginning of each session. There were a total of 104 practice trials from all attention conditions (focused/divided), coherence levels (high/low coherence level), motion directions (46 to 334° in 72° increments), and target color conditions (black/white). After practice, participants performed a block of calibration trials. Participants reported coherent motion consisting of 100% coherent dots using the flight simulator joystick. In each session, participants completed one block of 60 calibration trials (12 of each of the 5 possible motion directions).

Data Analysis. We first estimated how each participant responded to each of the 5 motion directions (46 to 334° in 72° increments) by computing circular medians of the participant's responses to each motion direction on the calibration trials (mean responses across controls and patients were 41.3, 127.5, 169.1, 250.6, and 303.5° for the motion directions of 46, 117, 189, 261, and 333° , respectively). These calibrated angles were later used as participant-specific baselines to compute performance accuracy on the test trials for each participant.

For each test trial in the main task, we first computed at each time point how far the joystick had moved from the center (response trajectory). We next identified the coordinate of the joystick at its maximum distance from the starting point and used that value to compute the angle in degrees from the starting point to the end point. We then computed the difference between the response angle at each time point and the calibrated response at each time point (response error). Response errors could be recorded even before the joystick began moving toward the end point, based on the direction in which the joystick was oriented. Test trials where responses were either made after the response deadline or where the response errors at the joystick's maximal distance were more than 150° were excluded from further analysis.

We also examined the effect of coherence level (low/high), attention (focused/divided), and expectation (expected/unexpected) on response trajectories

Table 2. Neuropsychological scores for memory-impaired patients

Patient	Prose recall, segments	Diagram recall	Paired-associate learning, pairs
D.A.	3	9	13
K.E.	0.5	4.5	2
L.J.	0	5	0
G.W.	0.5	3	0

and response errors across time. Finally, we asked whether each patient's performance conformed to control performance by comparing response trajectories and response errors of each patient with the control averages.

Statistical Procedures. Due to the small number of participants (10 controls and 4 patients), a bootstrapping procedure was performed to assess significant differences between conditions and to establish 95% confidence intervals. Specifically, each of the bootstrapping iterations was performed by resampling with replacement at the level of individual trials and computing means for each comparison of interest. All reported confidence intervals (CIs) were computed based on 1,000 bootstrapping iterations for each comparison. Note that this method constrains the resolution of P values to a lower limit of $P \leq 0.001$. We generated permuted null distributions of response trajectories and response errors for each participant, each condition, and

each time point. For tests comparing a bootstrapped distribution against 0, P values were computed by conducting 2 one-tailed tests against 0 (e.g., mean[difference in response trajectories < 0] and mean[difference in response trajectories > 0] and doubling the smaller P value).

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