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Can amnesic patients learn without awareness? New evidence comparing deterministic and probabilistic sequence learning

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Abstract

Can associative learning take place without awareness? We explore this issue in a sequence learning paradigm with amnesic and control participants, who were simply asked to react to one of four possible stimuli on each trial. Unknown to them, successive stimuli occurred in a sequence. We manipulated the extent to which stimuli followed the sequence in a deterministic manner (noiseless condition) or only probabilistically so (noisy condition). Through this paradigm, we aimed at addressing two central issues: first, we asked whether sequence learning takes place in either condition with amnesic patients. Second, we asked whether this learning takes place without awareness. To answer this second question, participants were asked to perform a subsequent sequence generation task under inclusion and exclusion conditions, as well as a recognition task. Reaction times results show that amnesic patients learned the sequence only in the deterministic condition. However, they failed to be able to reproduce the sequence in the generation task. In contrast, we found learning for both sequence structures in control participants, but only control participants exposed to a deterministic sequence were successful in performing the generation task, thus suggesting that the acquired knowledge can be used consciously in this condition. Neither amnesic nor control participants showed correct old/new judgments in the recognition task. The results strengthen the claim that implicit learning is at least partly spared in amnesia, and the role of contextual information available for learning is discussed.

Keywords: Amnesia; Sequence learning; Awareness

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1. Introduction

Whether associative learning can take place without awareness is a central issue for the cognitive neurosciences. Amnesic patients, whose explicit memory is severely impaired, provide us with a unique opportunity to explore this issue. In this paper, we explored the extent to which such patients are able to learn about the regularities contained in deterministic or probabilistic sequences of events presented visually in the context of a choice reaction time task – a robust paradigm known as sequence learning, and in which incidental learning has been abundantly documented, both with normal participants (Nissen & Bullemer, 1987; Cleeremans & McClelland, 1991; Reed & Johnson, 1994) as well as with special populations (Nissen & Bullemer, 1987; Reber & Squire, 1998). In the following, we first provide an overview of the contribution that studies of amnesic patients can bring in the debate concerning the possibility of learning without awareness. Next, we focus on the sequence learning paradigm itself, and finally on the comparison between deterministic and probabilistic sequence learning.

1.1. Amnesic patients studies: evidence for learning without awareness?

The possibility that learning may occur without awareness remains a controversial issue (Shanks & St. John, 1994; Cleeremans & Jiménez, 2002; Perruchet & Vinter, 2002). The most compelling evidence for the existence of two distinct and independent systems has been accumulated in studies with amnesic patients. Indeed, while their declarative or explicit memory is poor, amnesic patients exhibit intact learning in various tasks of non-declarative memory, such as eye blink con-

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ditioning (albeit only under so-called delay conditioning, that is, when conditional and unconditional stimuli overlap in time, Clark, Manns, & Squire, 2002), perceptual priming (Hamann & Squire, 1997) or procedural skills, such as manual pursuit rotor task (Brooks & Baddeley, 1976) or mirror tracing (Milner, Corkin, & Teuber, 1968; Cohen & Squire, 1980). In all these situations, previously encoded information influences amnesic patients' behaviour in the absence of conscious recollection, suggesting that learning can take place without awareness.

More controversial findings were obtained with probabilistic classification tasks, in which subjects learned which of two outcomes would occur on each trial, given the particular combination of cues that appeared. Amnesic patients performed similarly to matched controls on such tasks, at least over the first 50 training trials, but they also exhibited a severe impairment in declarative memory in a subsequent test (Knowlton, Squire, & Gluck, 1994; Knowlton, Mangels, & Squire, 1996). However, Hopkins et al. (2004) showed that amnesic patients with bilateral hippocampal damage due to hypoxia exhibited an early and lasting deficit on two probabilistic learning tasks involving easily discriminable categories. Moreover, it was shown that patients used simpler and degenerate learning strategies, in which they learn the correct answer to a few easy patterns and guess on the rest. This suggests that medial temporal damage affects probabilistic category learning, at least in some amnesic aetiologies.

Some arguments that reinforce the idea that learning can occur unconsciously were also obtained in one of the main paradigms through which to study implicit learning, namely artificial grammar learning (Reber, 1967). Amnesic patients were able to learn about and classify strings of letters generated from a finite-state grammar as accurately as healthy participants, but their recognition of the training strings was impaired (Knowlton & Squire, 1996), or they were unable to generate them in a direct manner (Meulemans & Van der Linden, 2003). Again, these results suggest the existence of two separate learning systems: an implicit or non-declarative system on the one hand, and an explicit or declarative system, on the other hand. This second system would be impaired in amnesia. It is important to note that this view of the functional role that hippocampus and the medial temporal lobe play in learning remains controversial. Recent simulation results (Kinder & Shanks, 2001) indeed suggest that a single-system connectionist model in which the functional deficits associated with amnesia are captured by a reduced learning rate could predict the pattern of results obtained by Knowlton and Squire. As a result, Kinder and Shanks assume that it is not necessary to assume the existence of two separate memory systems to explain the observed dissociation between classification and recognition tasks. The performance of amnesic patients in memory tasks would thus be better understood in terms of a non-selective deficit of a single explicit learning system. Many relevant studies have been conducted using the serial reaction time (SRT) task, which we overview in the next section.

1.2. Sequence learning and amnesia

As in the artificial grammar paradigm, sequence learning studies performed with amnesic patients suggest that they can learn a repeating sequence while remaining unable to consciously recognize it (Curran, 1997; Reber & Squire, 1998). However, we do not know whether amnesic patients can also learn probabilistic (or noisy) sequences, and we only have little information about the implicit or explicit nature of the knowledge acquired during the SRT task. In a typical sequence learning experiment, participants first perform a serial reaction time task (Nissen & Bullemer, 1987), in which they are asked to react to each element of a sequentially structured and typically visual sequence of events. On each trial, they see a stimulus appear at one of several locations on a computer screen and are asked to press on the corresponding key as fast and as accurately as possible. Unknown to them, the sequence of successive stimuli follows a repetitive pattern. Reaction times (RTs) tend to decrease progressively during practice but to increase dramatically when the repetitive pattern is modified in any of several ways (Reed & Johnson, 1994; Shanks & Johnstone, 1999; Destrebecqz & Cleeremans, 2001). This finding suggests that healthy participants learn the pattern and tend to respond on the basis of their knowledge of the sequence. However, the extent to which the acquired knowledge is implicit or explicit remains controversial.

To address this issue, and based on the central assumption that any task will always tend to involve both implicit and explicit influences, Destrebecqz and Cleeremans (2001) adapted the Process Dissociation Procedure (Jacoby, 1991) to sequence learning. To probe participants' knowledge of the sequential material after training on the SRT task was completed, they used a so-called "free generation" task – previously shown to be a very sensitive test of sequence knowledge (Perruchet & Amorim, 1992).

After performing the SRT task, participants were informed about the presence of a sequence in the task they had just performed and were required to freely generate a sequence under inclusion and exclusion instructions. Under inclusion instructions, participants were asked to reproduce the sequence as much as possible. This is a facilitation task because both explicit and implicit knowledge may help participants generate the sequence on which they have been trained. Under exclusion instructions, in contrast, participants were instructed to generate a different sequence, and to avoid reproducing the training sequence. This is an interference task because explicit and implicit knowledge of the repetitive pattern act in opposition: only explicit knowledge can help participants reproduce the repetitive pattern to improve their performance. If the repetitive pattern is nevertheless produced under exclusion instructions, such responses can only be interpreted as reflecting the implicit influence of learned sequential regularities. Finally, participants perform a recognition task on fragments of the training sequence (Perruchet & Amorim, 1992) to assess the extent to which sequence knowledge is available to consciousness. By using this methodology, Destrebecqz and Cleeremans (2001) showed that sequence learning could be implicit with healthy participants, under some specific temporal conditions (i.e., when they were denied preparation to the next stimulus – that is, when the interval that separates participants' responses and the onset of the next stimulus was eliminated. However, for a failure to replicate, see Shanks, Wilkinson, & Channon, 2003; Wilkinson & Shanks, 2004).

In the present experiment, we sought to adapt Destrebecqz and Cleeremans (2001) methodology to the study of amnesic participants. In addition, we compared learning under two conditions defined by the nature of the sequential material. The sequential material could indeed either consist of a repeating deterministic sequence (noiseless condition) or of a comparable probabilistic sequence (noisy condition). We describe and motivate these conditions in the next section.

1.3. Deterministic and probabilistic sequence learning

Typically, the structure of the repetitive pattern used in the SRT task is either deterministic (noiseless) or probabilistic (noisy). Under deterministic conditions, a fixed sequence of stimulus positions is repeated all through the SRT task, except during a transfer block in which a different sequence is presented. In most experiments, the fixed sequence and the transfer sequence are composed entirely of second-order conditionals (SOC, Reed & Johnson, 1994), in which (1) every location that the target can visit is fully determined by the previous two locations and (2) knowing the previous location alone provides only limited information regarding the next location. Early studies revealed that RTs tend to decrease with practice and to increase during the transfer phase, leading authors to conclude that participants exhibit sequence-specific learning.

The major limitation of using fixed sequences of events in the context of implicit learning research is that participants tend to learn parts of the repeated sequence explicitly (Perruchet & Amorim, 1992; Cleeremans & Jiménez, 1998). This led some authors to introduce noise in the repeated sequence so as to make conscious detection of sequential structure much more difficult. Cleeremans and McClelland (1991) first introduced such sequences by using material generated based on a probabilistic finite-state grammar. More recently, Schvaneveldt and Gomez (1998) developed a probabilistic version of deterministic SOC sequences by manipulating the conditional probabilities of transitions. For instance, the sequence fragment 1–4 could be followed by Location 3 with a probability of 0.90, and by Location 2 with a probability of 0.10 (whereas in the deterministic SOC sequence, 1–4 was followed by Location 3 with a probability of 1.00). Schvaneveldt and Gomez showed that healthy participants were able to learn about the probabilistic structure of sequences, as shown by lower error rates and faster RTs to highly probable as compared to less probable transitions.

Comparing deterministic and probabilistic material is interesting both in healthy participants and in amnesic patients. Indeed, we assume that the noiseless and repeating character of the deterministic sequence makes it possible for *healthy participants* to acquire more explicit knowledge than in under probabilistic conditions. This knowledge can be subsequently assessed using direct measures such as generation and recognition tasks. The only experiment using the same probabilistic sequences as Schvaneveldt and Gomez and a subsequent recognition task noted a learning effect with healthy participants, and showed that the participants were able to recognize 6-elements sequences from the 12-elements training sequence (Shanks et al., 2003, experiment 3).

Moreover, if we assume that probabilistic sequences lead *amnesic patients* to acquire knowledge that is less available to consciousness than when learning deterministic sequences, we may wonder whether they would still be able to exhibit sequence learning effects during the SRT task. Probabilistic sequences (Schvaneveldt & Gomez, 1998) offer the possibility of examining anticipation errors (i.e., when a response that is appropriate for a highly probable transition is produced after a less probable transition), which would be particularly informative about the nature of what is learned by amnesic patients. We stated that under deterministic sequence learning conditions, previous experiments using SOC sequences with amnesic patients had revealed significant learning effects (Reber & Squire, 1994, 1998; Curran, 1997), although no explicit recognition of the repeated pattern was found in the amnesic groups, in contrast to the control groups (Reber & Squire, 1994, 1998). This dissociation led authors to consider that learning in this situation was implicit in amnesic patients. Only two studies using different types of probabilistic material have been performed with amnesic patients. First, Cleeremans (1993, Chapter 4) reported on an amnesic patient exposed to a probabilistic sequence generated from an artificial grammar and found a learning effect similar to that of the control participants. Second, Curran (1997) showed that amnesic patients were able to learn "FOC" sequences ("first-order conditionals", in which elementary associations between adjacent stimuli may be predicted: each element is followed by another element in a 67/33 ratio). However, no probabilistic sequence learning study has investigated performance in amnesic patients with the Schvaneveldt and Gomez (1998).

To sum up, in this experiment, severely memory impaired patients and control participants first performed an SRT task (with a deterministic or probabilistic sequence) and then two direct tasks (generation and recognition) to assess the extent to which knowledge acquired during the SRT task is available to conscious awareness. This study was thus aimed at addressing two central questions. First, we wondered whether learning is preserved in amnesia, in either deterministic or probabilistic conditions. Previous studies (Reber & Squire, 1994, 1998; Curran, 1997) suggest that amnesic patients exhibit implicit learning under deterministic conditions, but to the best of our knowledge, no study has compared deterministic and probabilistic sequence learning in amnesia. Second, if amnesic patients acquire sequential knowledge during the SRT task, we wondered whether this knowledge is available to consciousness. The methodology proposed by Destrebecqz and Cleeremans (2001), with a generation task following inclusion and exclusion instructions and a recognition task, should allow us to obtain more information concerning this second issue.

2. Method

2.1. Subjects

Six individuals with anterograde amnesia and 24 matched control participants took part in the study. They were all unfamiliar with the SRT task. Amnesic

Table 1
Demographic data, diagnosis informations and results of the amnesic patients in the Raven's Progressive Matrices (PM38), the Spans and the Executive Functioning tasks

Patient	Age	Sex	ED	Aetiology of cerebral damage	Time since diagnosis	PM38 (percentiles)	Span			Executive functioning				
							Verbal		Spatial	Stroop test			Hayling test	
							Direct	Reverse		Naming time (errors)	Reading time (errors)	Interference time (errors)	Error (type 1)	Error (type 3)
JMD	49	Male	9	Korsakoff syndrome	3 months	50	4	4	4	90 s (0)	60 s (0)	240 s (5C, 7NC)	**8**	0
GR	43	Male	15	Rupture of anterior communicating artery aneurysm	2 months	25	4	3	5	**105 s (5C)**	65 s (**2C**)	**275 s** (**10C**, **20NC**)	**10**	0
HV	51	Female	15	Korsakoff syndrome	12 years	25	6	6	4	70 s (0)	48 s (0)	127 s (2C, 1NC)	**9**	0
BC	41	Female	12	Korsakoff syndrome	5 years	25	4	4	4	61 s (0)	45 s (0)	104 s (0)	7	1
MO	47	Female	15	Korsakoff syndrome	16 years	10	7	5	4	67 s (0)	53 s (0)	95 s (1C)	7	0
AC	44	Male	19	Closed-head trauma	15 years	95	5	5	4	–	–	–	3	0

Note: "ED", years of formal education. In the Stroop test, "C", number of self-corrected errors and "NC", number of uncorrected errors. AC did not performed the Stroop test because of colour-blind. In the Hayling test, error of type 1 correspond to the response semantically related to the expected word and error of type 3 correspond to the expected word itself. Bold scores are below two standard deviations under the normal mean performance.

patients included four Korsakoff patients, one patient who had suffered a ruptured aneurysm of the anterior communicating artery, and one closed-head injury patient. Table 1 shows clinical information about the patients, as well as their global intellectual efficiency (tested with Raven's Progressive Matrices, Raven, 1938), their verbal and spatial spans and their results on executive functioning tasks. We can see that all patients showed global intellectual efficiency and verbal and spatial spans within the normal range. To measure their inhibition capacities, all patients performed the Stroop test and the verbal inhibition Hayling test. Results presented in Table 1 suggest that the executive functioning of some patients was not completely intact (see GR in the Stroop task, or HV, GR or JMD in the Hayling test). However, clinical observations revealed that these patients were forgetting the instructions during the task itself, so that scores should be taken cautiously. Moreover, our results (see below) show that these deficits did not interfere with the generation performance of these patients. Lastly, measures of attentional capacities were taken during the SRT task itself (described below) and revealed that in none of the patients, any attentional deficit interfered with the experiment.

To assess their degree of amnesia, all patients were given various tests of immediate and delayed recall, such as the "Grober and Buschke's Test" (Grober & Buschke, 1987) for verbal learning and "Test de la Ruche" (Violon & Wijns, 1984) for visuo-spatial learning or "Doors Recognition Test" (Baddeley, Emslie, & Nimmo-Smith, 1994) for pictural memory. Results are presented in Table 2. The *Grober and Buschke's Test* is a verbal learning task in which 16 to-be-learned words were presented to the patients, with semantic encoding being running for four words at a time. The "recall phase" of the 16 words included three trials. Each trial consisted of an extended period of free recall ("Free recall 1–2–3"; up to 2 min), immediately followed by cued recall for those items not retrieved at free recall (the category cue of each of those was verbally provided). Patients also performed a recognition task amongst 48 words and a delayed recall (after a 20 min delay). The "*Test de la Ruche*" is a visuo-spatial learning task in which patients have to learn the position of 10 black boxes in a 41 boxes-matrix. The learning phase included five trials ("Recall 1–2–3–4–5"). In the "Recognition phase", nine matrices were presented to the patients who had to recognize the one they had to learn. A "Delayed Recall phase" occurred after a 10 min delay. The "*Doors Recognition Test*" is a visual recognition task in which patients had to watch 24 door pictures and then to recognize them amongst other door pictures. Results presented in Table 2 show the number of positions correctly recalled or recognized in the "Test de la Ruche", and the number of pictures correctly recognized in the "Doors Recognition Test". Table 2 show that all patients exhibited recall and recognition performance on the verbal learning task well below two standard deviations under the controls' mean performance, as well as on the visual memory measurements. We also checked that patients did not have visual impairments preventing them from perceiving precisely the whole screen.

Participants were randomly assigned to deterministic and probabilistic conditions. Amnesic patients were also subjected to a second session, taking place at least 5 weeks after the first session, during which they performed the alternate experimental condition (deterministic or probabilistic). We took precautions to assess any interference effect from the first experiment on the second one (described below). We also checked that their memory impairment remained stable during the whole experimental period by giving them a parallel version of the "Grober and Buschke's Test" before the second experimental session, in those cases where the time since diagnosis was less than 2 years. This was the case for JMD and GR, but as they performed similarly in the parallel version we do not describe the results. Because participants were debriefed about the repetitive sequence before completing the generation and recognition tasks, control participants could reasonably be expected to remember the debriefing across sessions (see Curran, 1997). Therefore, each control participant was only tested in a single condition (either deterministic or probabilistic). Four control participants were matched to each amnesic patient (two exposed to the deterministic sequence and two exposed to the probabilistic one) in terms of sex, age and level of education. Control participants volunteered and were screened via self-reports for absence of any existing neurological or psychiatric condition and for absence of any medication that could affect cognition. All participants received oral information about the experiment and gave their approval orally or signed statements of informed consent prior to testing.

Table 2
Results of the amnesic patients in the long-term verbal and visual memory measurements

Patient	Verbal memory measurements (Grober and Buschkel)						Visual memory measurements							
	Free recall 1 (free + cued recall 1)	Free recall 2 (free + cued recall 2)	Free recall 3 (free + cued recall 3)	Delayed free recall (delayed free + cued recall)	Recognition	False recognition	"Test de la Ruche"							
							Perception	Recall 1	Recall 2	Recall 3	Recall 4	Recall 5	Recognition	Delayed recall
JMD	−3.9 (<Perc. 1)	−4.9 (<Perc. 1)	−5.2 (<Perc. 1)	−5.9 (<Perc. 1)	**10**/16	**2**	10/10	4/10	**0**/10	**3**/10	**6**/10	**2**/10	?	**0**/10
GR	−4 (<Perc. 1)	−4.6 (<Perc. 1)	*	*	*	*	10/10	**1**/10	**0**/10	**3**/10	**2**/10	*	*	*
HV	−3 (<Perc. 1)	−4.1 (<Perc. 1)	−5.2 (<Perc. 1)	−5.9 (<Perc. 1)	**14**/16	**9**								
							"Doors Recognition Test"							
							Scores	Percentiles						
BC	−3.3 (Perc. 1–5)	−4.8 (<Perc. 1)	−5.4 (<Perc. 1)	−6.2 (<Perc. 1)	**7**/16	1	**14**/24	1–5						
MO	−2.9 (Perc. 1)	−4.9 (<Perc. 1)	−5.2 (<Perc. 1)	−6.3 (<Perc. 1)	**8**/16	1	**9**/24	<1						
AC	−2.7 (<Perc. 1)	−4.8 (<Perc. 1)	*	*	**7**/16	**12**	**7**/24	<1						

Note: "Free recall 1–2–3" scores was determined by the number of standard deviations from the mean of words correctly evoked on the three successive trials. "Free + cued recall 1–2–3" scores was determined by the percentiles corresponding to the number of words correctly evoked at free + cued recall on the three successive trials. Normative data with age and educational level come from Van der Linden et al. (2004). Bold scores are below two standard deviations under the normal mean performance. The mark "*" means that the task had been stopped because of the patient's difficulties; "?" means that the patient did not answer the question.

2.2. *Procedure*

The first part of the experiment consisted of a serial reaction time task. After this task, participants performed two free generation tasks (one under, "inclusion" instructions and one under "exclusion" instructions), and a recognition task.

During the *SRT task* (Nissen & Bullemer, 1987), a stimulus appeared on each trial at one of four possible screen locations arranged horizontally on a computer screen. Participants were instructed to respond as fast and as accurately as possible by pressing on one of four corresponding keys organized in a spatially compatible manner. The target was removed as soon as a key had been pressed, and the next stimulus appeared after a 250 ms interval. Erroneous responses were signalled to participants by means of a tone. Participants did not have to correct their responses. Participants performed 60 random training trials, followed by 18 or 21 experimental blocks of 96 trials (for the deterministic and probabilistic conditions, respectively) during which, unknown to them, the stimulus followed a regular location sequence (the "training sequence"). Short rest breaks occurred between experimental blocks. Each block began at a random point in the sequence. For each trial, reaction times and responses were recorded.

Two 12-element sequences were used in the SRT task. These sequences consisted entirely of so-called "second-order conditional" transitions (Reed & Johnson, 1994). Both sequences included four distinct elements ("1", "2", "3" and "4"), corresponding to the four possible locations on the screen (SOC1 = "3–2–4–1–3–4–2–3–1–2–1–4" and SOC2 = "3–2–3–4–1–2–4–3–1–4–2–1"). The sequences were equated with respect to location frequency (each location occurred three times), first-order transition frequency (each location was preceded once by each of the other three locations), repetitions (no repetition in either sequence) and reversal frequency (one in each sequence; e.g., "1–2–1"). The only difference between the sequences was in terms of the sub-sequence of three-elements that they contained. For instance, the transition 1–4 was always followed by Location 3 in SOC1 and by Location 2 in SOC2. In each condition, half the participants were trained on SOC1 and the other half on SOC2. Moreover, the amnesic patients trained on SOC1 for the first experiment were then trained on SOC2 for the second one, and conversely for the others.

2.2.1. *Deterministic condition*

The experiment consisted of 18 experimental blocks of 96 trials for a total of 1728 trials. Each block consisted of eight repetitions of the sequence. Block 16 was the transfer block: the training sequence (grammatical trials) was replaced by the transfer sequence (non-grammatical trials). Thus, participants trained on SOC1 during the first 15 blocks were exposed to SOC2 during block 16 and then to SOC1 again during blocks 17 and 18. This design was reversed for the other half of the participants. Increased RTs during block 16 were thus expected only when participants had acquired SOC knowledge during training over blocks 1–15.

2.2.2. *Probabilistic condition*

The experiment consisted of 21 experimental blocks of 96 trials for a total of 2016 trials (more experimental blocks were necessary to expose participants to the same number of grammatical trials number in both deterministic and probabilistic conditions). For each block, the probabilistic sequences were implemented as in Schvaneveldt and Gomez's experiment (1998): the two most recent locations were used to select the next location. Thus, with probability 0.80, the next location would be the location in the training sequence following the previous two locations, and with probability 0.20, the next location would be the location in the transfer sequence which followed the previous two locations. Thus, participants trained on SOC1 were exposed in 80% of the trials to the second-order transitions of SOC1 and in 20% of the trials to those of SOC2. This design was reversed for the participants trained on SOC2. As a consequence, in the probabilistic condition, transfer stimuli were interspersed with training stimuli throughout the whole task, whereas all such transfer items appeared only during the transfer block under deterministic conditions.

Following the SRT task, participants were informed that the stimulus had followed a repeating sequence. They were then asked to perform *a free generation task* (Perruchet & Amorim, 1992; Destrebecqz & Cleeremans, 2001), under two conditions. First, in the "inclusion condition", they were presented with a stimulus appearing at any of the four locations, and asked to freely generate a series of 95 trials that “resembled the training sequence as much as possible”. The stimulus moved whenever participants had pressed one of the keys, and appeared at the corresponding location after a delay of 250 ms. They were told to rely on their intuitions when feeling unable to recollect the location of the next stimulus. Second, they were asked to generate another sequence of 95 trials, now following exclusion instructions (that is, avoiding the reproduction the sequential regularities of the training sequence). In both generation tasks, participants used the same keys as in the SRT task, and were told not to repeat responses. They were not instructed to respond as fast as possible, and did not receive any feedback about their responses.

After completion of the generation tasks, participants performed a *recognition task* (Shanks & Johnstone, 1999). They were presented with 24 fragments of three trials and asked to react to the stimuli as in the SRT task, and then to provide a rating of how confident they were that the fragment was part of the training sequence. Twelve fragments were part of the training sequence, and 12 were part of the transfer sequence. Fragments were divided up randomly. Ratings involved a six-points scale (1, “I’m certain that this fragment was part of the training sequence”; 2, “I’m fairly certain that this fragment was part of the training sequence”; 3, “I believe that this fragment was part of the training sequence”; 4, “I believe that this fragment was not part of the training sequence”; 5, “I’m fairly certain that this fragment was not part of the training sequence” and 6, “I’m certain that this fragment was not part of the training sequence”). Both ratings and RTs were recorded.

2.3. *Previous experiment knowledge assessment*

Before the second experiment, amnesic patients were asked a series of questions to assess their memory of the experiment they had performed 5 weeks earlier (e.g., Had they seen the apparatus before? What had appeared on the screen? What was the goal of the task?). Next, they were presented with the same pattern on the screen as in the previous experiment (a stimulus that appeared in any of the four locations) and they were asked once again what the goal of the task was. None of the patients was able to recall what they were asked to do 5 weeks earlier, even when the very same stimulus display used during the first session was shown again on the computer screen. Then, they were asked to freely generate a series of 95 trials. Results are presented in Table 3, and show that 5 weeks after the first experiment, patients did not generate more training triplets than expected by chance level (50%). Following this previous knowledge assessment, amnesic patients had to perform the SRT task, the two-generation tasks and the recognition task as in the first experiment (but in the alternate condition).

2.4. *Material*

The experiment was run on a Macintosh PowerBook 5300c portable computer with an additional keyboard for better comfort. The display consisted of four dots arranged in a horizontal line on the computer’s screen and separated by intervals of 4 cm. These dots remained on the screen during all the experiment. Each screen position corresponded to a key on the computer’s keyboard (“v”, “b”, “n” and “,”). The spatial configuration of the keys was fully compatible with the screen positions. Participants were told to put the index and middle fingers of each hand on these keys and to let them until the end of the experiment (except during the breaks). The stimulus was a small black circle 0.35 cm in diameter that appeared on each trial on a white background, centred 1 cm below one of the four dots.

Table 3
Results of the amnesic patients on the previous tests

Patient	Previous test	
	Before first experiment (%)	Before second experiment (%)
JMD	–	53
GR	–	48
HV	56	59
BC	–	43
MO	50	50
AC	42	47

Note: Scores represent percentages of generated triplets that were part of the training sequence. As in the generation task, we computed only training and transfer triplets, so that chance level is 50%. The mark “–” means that the patient did not perform the test.

3. Results

In all analyses, a significance criterion of $\alpha = .05$ was used.

3.1. *SRT task*

We calculated mean RTs by block, for each group of participants (amnesic versus control) and for each condition (deterministic versus probabilistic). RTs associated with the first two stimuli of each block were excluded, because their locations could not be predicted. RTs associated with erroneous responses were also excluded, as were RTs beyond two standard deviations above the subject mean per block. The percentages of excluded RTs were around 5% in each condition, and did not differ between amnesic and control groups, neither in the deterministic condition [$t(16) = -.515$, $p > .5$, two-tailed], nor in the probabilistic condition [$t(5.178) = .216$, $p > .5$, two-tailed]. This suggests that in none of the patients, any attentional deficit interfered with the experiment. As the two subgroups of participants presented, in both conditions, with either SOC1 or SOC2, were trained identically and performed similarly, their RTs were combined for subsequent analyses.

3.1.1. *Deterministic condition*

3.1.1.1. Reaction time analyses. Fig. 1 shows the average RTs obtained over the entire SRT task with a deterministic sequence plotted separately for amnesic and controls participants. Prior to each analysis of variance (ANOVA), data were tested with Mauchly’s test of sphericity. Where sphericity was of concern, the degrees of freedom were modified with the Greenhouse–Geisser epsilon and effects are reported significant according to the adjusted alpha

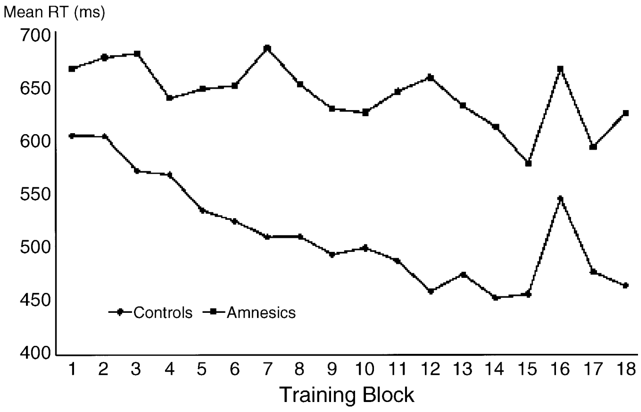

Fig. 1. Mean reaction times (RT) in milliseconds accross blocks in the SRT task with a deterministic sequence, plotted separately for amnesic and control participants.

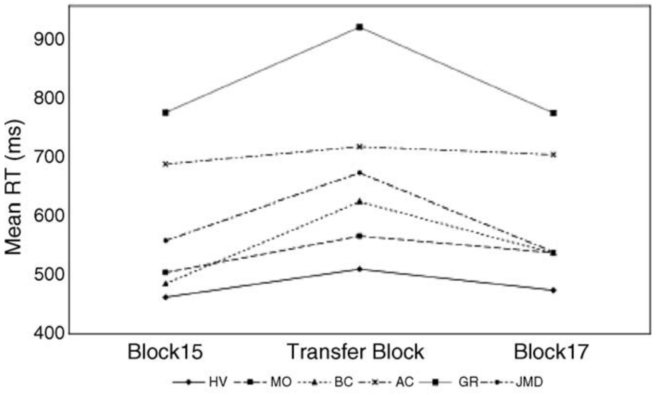

Fig. 2. Transfer effect in milliseconds in the SRT task, plotted separately for the six amnesic patients.

level. An ANOVA with Training Blocks (15 levels, the first 15 blocks) as a within-subjects variable and Group as a between-subjects variable revealed significant effects of Training Blocks [$F(5.987,95.785) = 9.57$, MSE = 47700.49, $p < .001$] and Group [$F(1,16) = 6.23$, MSE = 991199.11, $p < .05$]. The interaction also reached significance [$F(5.987,95.785) = 2.85$, MSE = 14230.439, $p < .05$]. Next, independent ANOVAs conducted on both control and amnesic groups revealed a significant effect of Training Blocks for control participants [$F(4.541,49.949) = 17.33$, MSE = 93399.281, $p < .001$], but not for amnesic patients [$F(3.226,16.13) = 1.58$, MSE = 20461.235, $p > .1$]. Thus, RTs decreased during the first 15 blocks of the SRT task in both groups, but the decrease was significant only in the control group.

Most importantly, RTs increased in both groups when participants were exposed to the transfer sequence on block 16. Further, presenting participants with the training sequence anew on blocks 17 and 18 allowed them to recover their pretransfer performance level. This observation was confirmed by another ANOVA with Transfer (two levels, block 16 and mean of blocks 15 and 17) as a within-subjects variable and Group as a between-subjects variable. This analysis showed significant effects of Transfer [$F(1,16) = 34.81$, MSE = 37539.87, $p < .001$] and Group [$F(1,16) = 5.64$, MSE = 98882.23, $p < .05$] but the corresponding Transfer × Group interaction failed to reach significance [$F(1,16) = 0.70$, MSE = 753.93, $p > .1$]. Thus, both groups are sensitive to the sequence modification, and the absence of interaction indicates that these learning effects are of similar extent. To probe the data more precisely, we checked directly that each of the amnesic patients had been sensitive to the sequence modification. Fig. 2 shows the transfer effect in the SRT task, plotted separately for each of the six amnesic patients. The figure shows that five of the six patient exhibit a transfer effect, that is, reacts more slowly when the sequence is changed. As transfer effects are not of similar extent for each patient, we computed the mean extent of the control group's transfer effect in order to verify that each of the patient performed like the control participants during the transfer phase. For the control group, we obtained a ratio between the transfer block RTS and the mean of the two adjacents blocks RTS of 1.18 (S.D. = 0.12; Min = 1.06 and Max = 1.52), and a ratio of 1.14 for the amnesic group (S.D. = 0.08; Min = 1.03 and Max = 1.22). That is, the patient with the smallest ratio was only 1.25 S.D. under the control group' mean ratio.

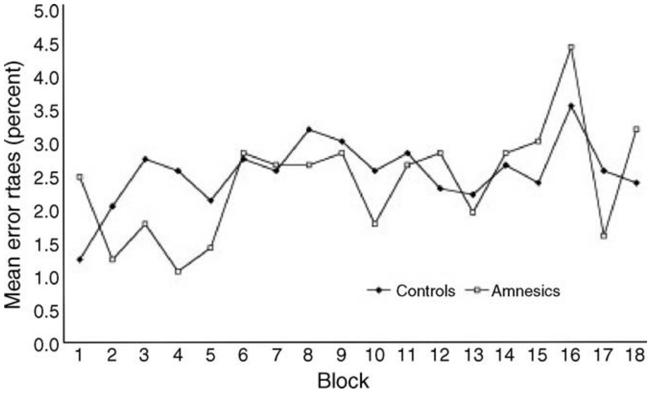

Fig. 3. Mean error rates (percent) across blocks in the SRT task with a deterministic sequence, plotted separately for amnesic and control participants.

3.1.1.2. Error analyses. Fig. 3 shows mean errors rates obtained over the entire SRT task with a deterministic sequence, plotted separately for the amnesic and control groups. An ANOVA showed only a significant effect of Transfer [two levels, block 16 and mean of blocks 15 and 17: $F(1,16) = 5.73$, MSE = 20.37, $p < .05$], but Group and the Transfer × Group interaction failed to reach significance (all $p > .5$). This confirms that mean error rates were higher during the transfer block than during adjacent blocks, for both amnesic and control participants. In the transfer block, the proportion of anticipation errors (that is, errors in which the training sequence response is produced when exposed to the transfer sequence) was 36% of the total errors for amnesic patients (32% of the total errors were repetitions errors and 32% were other errors), and 43% for control participants (19% of the total errors were repetitions errors and 38% were other errors).

We can thus conclude, both from RT and error analyses, that although amnesic patients were generally slower than their matched control participants, both groups have been disturbed by the sequence modification. No consistent decline in RTs' amnesic patients had been observed during the first 15 blocks, but error analyses suggest that amnesic patients behaved in a conservative manner: they committed few errors during the first 15 blocks (maximum 3%), suggesting that they privileged the precision with the detriment of the speed. Thus, although their RTs did not decrease significantly with practice, transfer block results show that amnesic patients, as well as their control participants, clearly learned the training sequence in the deterministic condition.

3.1.2. Probabilistic condition

3.1.2.1. Reaction time analyses. Fig. 4 shows mean RTs to highly probable (sequential) and less probable (noisy) transitions over the entire SRT task with a probabilistic sequence, plotted separately for amnesic and control participants. As described before, in the probabilistic condition, the non-grammatical stimuli were divided up all through the task, so that each group

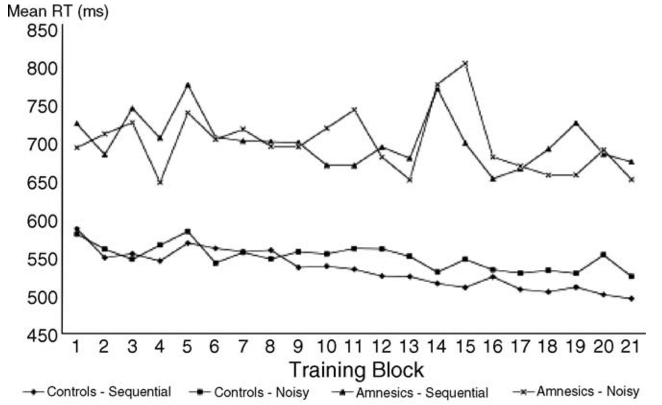

Fig. 4. Mean reaction times (RT) in milliseconds across blocks in the SRT task with a probabilistic sequence (80/20 ratio of sequential to noisy transitions), plotted separately for amnesic and control participants.

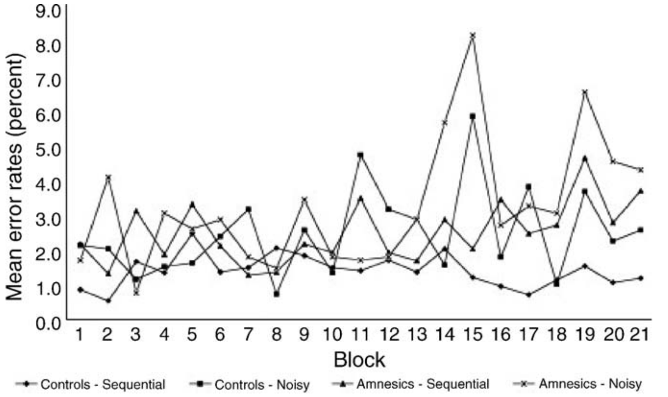

Fig. 5. Mean error rates (percent) across blocks in the SRT task with a probabilistic sequence (80/20 ratio of sequential to noisy transitions), plotted separately for amnesic and control participants.

is represented by two curves (for highly probable and less probable transitions, respectively). An ANOVA with probability (two levels, highly probable and less probable transitions) and Training Blocks (21 levels) as within-subjects variables and Group as a between-subjects variable revealed significant effects of Probability [$F(1,16) = 4.70$, MSE = 9805.81, $p < .05$] and Group [$F(1,16) = 5.19$, MSE = 4210698.1, $p < .05$]. Most important is the significant Probability × Group interaction [$F(1,16) = 5.50$, MSE = 1147.76, $p < .05$], which demonstrates that learning of the sequence was not of similar extent in amnesic and control groups. None of the remaining effects or interactions was significant (all $p > .1$). To measure learning effects in each group, two ANOVAs were conducted separately for control and amnesic groups. For the control group, the Probability × Training Blocks interaction reached significance [$F(5.139,56.53) = 2.62$, MSE = 7161.959, $p < .05$], revealing a greater probability effect later in practice than earlier (indicative of sequence learning). In contrast, the second ANOVA performed on amnesic patients' RTs, failed to reveal any significant effect (all $p > .1$), suggesting that amnesic patients did not learn the probabilistic material. Moreover, in contrast to the deterministic condition in which five on the six patients exhibited a learning effect, the observation of individual performance for each of the six amnesic patients shows that none of them exhibited a learning effect with probabilistic sequence.

3.1.2.2. Error analyses. Fig. 5 shows mean error rates to sequential and noisy transitions over the entire SRT task with a probabilistic sequence, plotted separately for the amnesic and control groups. Of particular interest, there was a significant effect of Probability [$F(1,16) = 6.80$, MSE = 145.12, $p < .05$], showing that more errors occurred on noisy transitions than on sequential ones. Neither the effect of Group nor other interactions reached significance (all $p > .1$). Thus, error rates seemed to evolve similarly in both groups.

The observation that more errors occur on less probable transitions suggests that participants have learned sequential transitions occurring with a higher probability and frequently make highly probable responses to less probable transitions. An additional analysis of the subset of errors called "wrong-sequence" errors (that is, the set of highly probable responses being made to the less probable transitions, also called "anticipation errors", or of the less probable responses being made to the highly probable transitions, see Schvaneveldt & Gomez, 1998) confirmed this inference: there were marginally significant effect of Probability [$F(1,16) = 3.67$, MSE = 41.15, $p < .075$], and significant effect of Training Blocks [$F(5.41,86.57) = 2.35$, MSE = 35.05, $p < .05$]. The Probability × Training Blocks interaction was marginally significant [$F(5.38,86.07) = 1.95$, MSE = 32.79, $p < .1$]. Neither the effect of Group nor other interactions reached significance (all $p > .4$). Participants of both groups were thus making increasingly more wrong-sequence errors to less probable than to highly probable transitions, hence engaging in anticipation behaviour. In contrast to the results of the RT data, which showed differences between amnesic and control groups in the probabilistic condition, the error data suggests similar learning for both groups.

We can thus conclude that amnesic patients showed sequence learning under deterministic conditions, and, to a much smaller extent under probabilistic conditions. In contrast, control participants showed sequence learning in both conditions. Before examining generation and recognition tasks results, we wondered if the first experiment would lead to a general procedural learning effect, so that each patient would begin the second experiment faster than he began the first one. An ANOVA on amnesic patients RTs during the five first blocks of the SRT task, for both experiments, revealed a significant effect of Order [$F(1,5) = 18.10$, MSE = 1130153.8, $p > .01$]. Neither the effect of Blocks nor the Blocks × Order interaction were significant (all $p > .1$). A detailed observation of individual performances confirms this order effect: all patients began the second experiment with faster RTs than in the first experiment, regardless of the structure of the sequence they were first exposed to. This suggests that 5 weeks after the first experiment, amnesic patients still showed a general procedural learning effect.

In the next section, we examine whether amnesic and control participants differ in their ability to project their knowledge of the sequence in generation and recognition tasks.

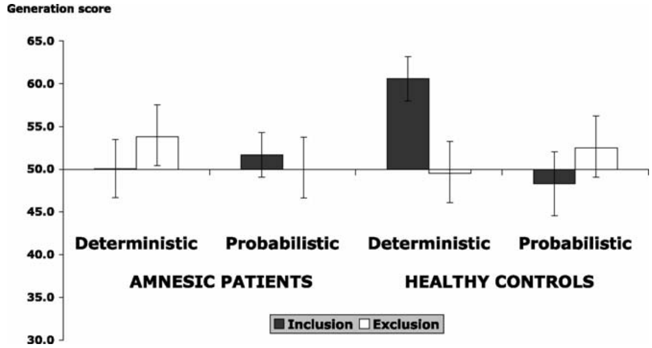

Fig. 6. Mean proportions of generated second-order conditional transitions (SOCs) that were part of the training sequence, plotted separately for amnesic and control participants, for both conditions, and under inclusion or exclusion instructions.

3.2. Generation tasks

In this generation task, participants were first asked to generate a sequence that resembles the training sequence as much as possible (inclusion instructions) and second to generate a different sequence, avoiding reproducing the training sequence (exclusion instructions). Even if amnesic patients did not always remember having performed the learning task, they were told to rely on their intuition under inclusion instructions and to try to counteract their intuition feelings under exclusion instructions. As the generation task is very similar to the SRT task, patients managed to perform it without difficulties. To measure generation performance, we computed the number of generated chunks of three-elements (triplets) that were part of the training sequence. To obtain inclusion and exclusion scores for each subject, we divided the corresponding number of correct triplets by the sum of the triplets that were part of the training sequence (correct triplets) and those that were part of the transfer sequence.[1] As only triplets from the training and from the transfer sequence were considered, chance level was .50.

Fig. 6 shows average inclusion and exclusion scores for both groups and both conditions. To find out whether generation performance reflects knowledge acquired during the SRT task, paired samples t tests were conducted to compare generation scores with those expected at chance level, that is, with the number of generated triplets that were part of the transfer sequence. Let us first examine the results of the *deterministic* condition (left panel of Fig. 6). Amnesic patients generated as many training triplets as transfer triplets under inclusion [$t(5) = -0.02$, $p > .5$, one-tailed] and exclusion instructions [$t(5) = -1.13$, $p > .1$, two-tailed]. In contrast, control participants generated more training triplets than transfer triplets under inclusion instructions [$t(11) = -2.01$, $p < .05$, one-tailed] but not under exclusion instructions [$t(11) = 0.19$, $p > .5$, two-tailed]. Concerning the *probabilistic* sequence (right panel of Fig. 6), both amnesic and control participants generated as many training triplets as transfer triplets under inclusion [$t(5) = -0.14$, $p > .5$; $t(11) = 0.95$, $p > .1$, one-tailed, for amnesic and control subjects, respectively] and exclusion instructions [$t(5) = -0.31$, $p > .5$; $t(11) = -0.66$, $p > .5$, two-tailed, for amnesic and control group, respectively]. This suggests that the generation performance of both amnesic and control participants after training under probabilistic conditions fails to reflect knowledge acquired during the SRT task. To summarize, only control participants exposed to a deterministic sequence generated a high percentage of correct triplets under inclusion instructions. Other generation scores were at baseline.

Moreover, an ANOVA with Group as a between-subjects variable, Condition (two levels, deterministic and probabilistic) and instructions (two levels, inclusion and exclusion) as within-subjects variables[2] only revealed a significant triple interaction between Group, Condition and Instructions [$F(1,16) = 5.83$, $\text{MSE} = 432.12$, $p < .05$; all other $p > .25$]. Independent ANOVAs on the amnesic group did not reveal any significant effect (all $p > .4$). By contrast, the ANOVA performed on the control participants generation scores revealed a significant interaction between Condition and Instructions [$F(1,11) = 8.49$, $\text{MSE} = 704.03$, $p < .05$; other $p > .25$]. Paired samples two-tailed t tests confirm that the control participants generated significantly more training triplets under inclusion than exclusion instructions under deterministic conditions [$t(11) = -2.38$, $p < .05$], but not under probabilistic conditions [$t(11) = 1.44$, $p > .1$]. Thus, control participants exposed to deterministic material were able to generate parts of the training sequence or to avoid reproducing them, according to the instructions. We can thus conclude that these participants have acquired explicit knowledge in the deterministic condition, but not in the probabilistic condition. In contrast, the generation performance of amnesic patients fails to reveal any learning, either in the deterministic or in the probabilistic condition.

One might wonder whether an inhibition deficit might interfere with our measures of implicit and explicit influences as computed in the generation task. Executive functioning of some patients was not indeed completely intact (see Table 1: GR in the Stroop task, or HV, GR or JMD in the Hayling test). However, in the generation task, each of these patients obtained a score that was below chance level under exclusion instructions, which indicates that they successfully avoided reproducing the training sequence. This is turn suggests that inhibition deficit is not a significant issue in our study.

3.3. Recognition task

Participants were asked to react to three-elements sequences (triplets) and to rate from 1 to 6 the extent to which they

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[1] As training and transfer sequences share the same abstract structure, this comparison allows us to make sure that generation performance reflects learning of the sequential contingencies of the training sequence and not merely basic frequency information (see Shanks & Johnstone, 1999; Destrebecqz & Cleeremans, 2001).

[2] Condition may be considered as a within-subjects factor because the same amnesic patients were exposed to both conditions and their control participants were paired two by two in terms of age, sex and education level (see Curran, 1997).

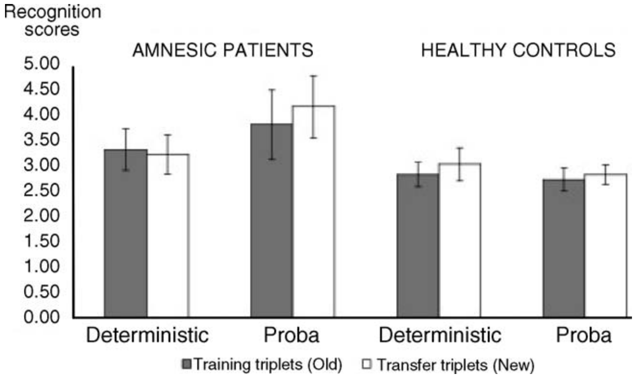

Fig. 7. Mean recognition ratings given for the 24 test triplets. A high rating (between 4 and 6) is expected for a new sequence, and a low rating (between 1 and 3) is expected for an old sequence.

felt these sequences were familiar. Sequences with erroneous responses were excluded. Mean recognition ratings for both conditions, both groups and both structures of sequence (old versus new) are shown in Fig. 7 (recall that high ratings correspond to judgments of novelty and are expected for triplets from the transfer sequence). An ANOVA performed on recognition ratings revealed no significant effect (all $p > .1$), except for Group [$F(1,14) = 3.66$, MSE = 5.86, $p < .08$], consistent with the amnesic group's tendency to generally use higher recognition ratings. Therefore, neither amnesic nor control participants were able to differentiate triplets from the training (old) and from the transfer (new) sequence.

Nevertheless, we compared, for each group, the mean RTs associated to the third element of the 12 training triplets with the mean RTs associated to the third element of the 12 transfer triplets.[3] One-tailed paired samples t tests showed that these differences were significant only for the control group [mean difference = 89 ms, S.D. = 155 ms, $t(11) = -1.98$, $p < .05$ and mean difference = 104 ms, S.D. = 179 ms, $t(11) = -2.02$, $p < .05$, for deterministic and probabilistic conditions, respectively]. This was not the case for the amnesic patients [mean difference = 32 ms, S.D. = 85 ms, $t(5) = 0.92$, $p > .1$ and mean difference = 279 ms,[4] S.D. = 540 ms, $t(5) = -1.27$, $p > .1$, for deterministic and probabilistic condition, respectively]. Hence, only control participants reacted significantly faster to the old than to the new triplets, suggesting perceptual fluency effects.

4. Discussion

In this study, we sought (1) to assess the extent to which amnesic patients can learn about probabilistic structure and (2) to assess the extent to which knowledge possibly acquired by such patients under incidental learning conditions is available to conscious awareness. To explore these issues, we compared the performance of six amnesic patients with that of 24 matched control participants in two conditions differing only in terms of sequence structure. In the deterministic (noiseless) condition, a standard 12-element sequence was repeated during the entire SRT task, while in the probabilistic condition, noise was introduced so as to prevent explicit learning. Each participant first performed an SRT task (with a deterministic or probabilistic sequence) and then two direct tasks (generation and recognition) assessing the extent to which the acquired knowledge is available to conscious control and to conscious recollection.

Our main results are as follows. The SRT task data revealed that in the deterministic condition, both amnesic and healthy participants were sensitive to a modification of the sequence, as evidenced by their transfer effect of similar extent both on RTs and errors rates. We observed that the RTs of five of the six amnesic patients increased when the sequence was changed. By contrast, in the probabilistic condition, only healthy participants exhibited faster RTs on sequential trials with practice, compared to non-sequential trials, indicative of sequence learning. Amnesic patients' RTs did not differ on these two types of trials. However, error analyses identified learning effects, both in amnesic and control participants.

In the generation task, only healthy participants exposed to the deterministic sequence were able to reproduce the sequence. Other scores were at baseline, suggesting that the knowledge acquired in the SRT task by healthy participants with a probabilistic sequence and by amnesic patients with a deterministic sequence was not strong enough to be projected in the generation task. Moreover, in the recognition task, regardless of the structure of the sequence participants had been presented with during the SRT task, neither amnesic nor control participants were able to explicitly differentiate between familiar and novel fragments. Nevertheless, control participants reacted faster to familiar fragments. To sum up, neither generation nor recognition data indicated any knowledge acquisition in the amnesic group, while they confirmed that control participants acquire more explicit knowledge under deterministic rather than probabilistic conditions.

Our results are congruent with previous findings (Reber & Squire, 1994, 1998; Curran, 1997) showing that amnesic patients can develop sensitivity to complex sequential knowledge when exposed to a repeated deterministic sequence. Furthermore, we found under probabilistic conditions, amnesic patients committed more and more anticipation errors with practice. This suggests that they can also develop sensitivity to complex sequential knowledge when exposed to a probabilistic sequence, as had already been suggested with other types of probabilistic materials (Cleeremans, 1993; Curran, 1997). Such learning has also been demonstrated in probabilistic classification tasks, in which amnesic patients performed similarly to matched controls, at least at the beginning of the task (see the weather forecast task, Knowlton et al., 1994, 1996). However, Hopkins et al. (2004) showed that learning was impaired when the probabilistic categories were more easily discriminable, suggesting that probabilistic learning is not always preserved in amnesia. In our

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[3] Indeed, as we know that two elements are necessary to predict the location of the third one, RT differences reflecting sequential knowledge can be observed only on the RT of the third element.

[4] Actually, the large mean and standard deviation in the amnesic group for probabilistic sequence are due to only one patient exhibiting extreme results. Results are the following after removal of this outlier: mean difference = 60 ms, S.D. = 75 ms and the RTs difference between old and new sequences becomes marginally significant [$t(4) = -1.815$, $p < .1$, one-tailed].

experiment, the finding that memory-impaired patients exhibit sensitivity to a probabilistic sequence through their error pattern but not through their reaction times is an interesting data point, but one that should be taken with caution because of the small percentage of errors.

Another interesting observation revealed by error analyses concerns the transfer phase in the deterministic condition, in which amnesic patients made fewer anticipation errors than healthy participants, but more repetitions errors. This observation may be explained by the role that explicit episodic memory can play in error elimination. Indeed, Baddeley and Wilson (1994) suggested that one of the major functions of explicit memory is the elimination of learning errors. In the case of normal participants, their explicit episodic memory of the learning experience can be called up in order to eliminate these errors on subsequent trials. In the absence of such explicit recollection, amnesic patients instead perseverate in making the same errors long after control participants have mastered the task. In our study, healthy participants may have learned the deterministic sequence in a more explicit way (pushing them to produce more anticipation errors when the sequence is changed). They may also have learned explicitly that no repetitions occurred during the task. In contrast, amnesic patients continue to make the same repetitions errors.

4.1. Preserved sequence learning in amnesia?

Our central goal in this study was to explore under which conditions amnesic patients exhibit preserved ability to learn about sequential regularities. Our results indicate preserved learning when the sequential material is deterministic but not when it is probabilistic. It is interesting to speculate about the differences between these two types of sequential structures. Beyond the obvious fact that probabilistic sequences are inherently more complex than deterministic ones, some authors have suggested that they are processed through different neural circuits. Peigneux et al. (2000), for instance, have suggested that the fixed and repeating associations between the elements of deterministic sequences make it possible for “encapsulated motor programs” (i.e., motor chunks) to be learnt in the basal ganglia, thus resulting in the observed speedup during the SRT task and the ensuing interference when the sequence is modified. In contrast, processing probabilistic sequences, which fail to contain as many stable, long chunks, would require the involvement of higher-order cognitive processes that are not so dependent on motor performance as when learning deterministic sequences. Such higher-order cognitive processes would thus be impaired in amnesia, while their motor abilities would remain relatively intact. Further research will need to find independent evidence to support this conclusion.

Another account of the better learning of deterministic sequences in both amnesic and control participants is based on the role of context. By assumption, participants in sequence learning tasks anticipate (consciously or not) the location where the next stimulus will appear so as to prepare their response even before the onset of the next stimulus. This preparation is necessarily based on the temporal context set by previous elements of the sequence. By construction, the contextual information conveyed by deterministic sequences is more predictive of forthcoming events than in probabilistic sequences. This account therefore predicts lower learning with probabilistic than with deterministic sequences (for contextual information is degraded in the former), and lower learning in amnesic patients than in control participants (for the latter have more difficulty memorizing contextual information), which is indeed what we found. This difference can also explain why learning tends to be more explicit for healthy participants when trained on deterministic material, for they can then acquire distinctive episodic traces of specific contexts, which is impossible under probabilistic conditions.

This account is also congruent with the results we obtained on the direct tests (generation and recognition) administered to participants after the SRT task. Both generation and recognition tasks require greater reliance on memorized contextual information than the SRT task itself. The facts that (1) healthy participants are able to express their knowledge during generation after exposure to deterministic material and (2) the fact that they exhibit perceptual fluency effects in the recognition task after having been trained either with deterministic or with probabilistic material are both indicative of the important role that context plays in modulating the extent to which sequence knowledge can be expressed. This stands in contrast with the generally poor performance observed when participants are asked to express old/new recognition judgments (contextual cuing is more important in generation and in reacting to short sequences in the recognition task, than in old/new recognition judgments). Both points thus reinforce the idea that tasks on which amnesic patients fail and those on which they perform normally may be best distinguished by the presence, or lack thereof, of context information (Nissen, Willingham, & Hartman, 1989). Indeed, whereas in most procedural skill learning tasks, the stimulus tightly constrains what response should be made, standard tests of recall and recognition memory fail to do so. Considered together, the graded character of our results, observed both over different sequential materials in healthy participants, and when comparing normal and amnesic performance across the different tasks, suggests (1) that the extent to which learned knowledge may be expressed depends on the amount and on the quality of contextual information available to participants and (2) that amnesia involves a deficit in our ability to bind together elements of the context in such a manner that high-quality traces associating the context with the appropriate response can be formed.

Finally, as each amnesic patient performed the experiment in both conditions, we were able to compare individual performance over the two sessions. We observed that 5 weeks after the first experiment, amnesic patients had forgotten the complex sequential knowledge they had learned over the first session, but they were nevertheless faster at the beginning of the second SRT session (which involved a different sequence). This suggests that procedural learning had been maintained over the 5 weeks interval, and confirms the preserved learning and retention of complex perceptual-motor skills in severe amnesia (Milner et al., 1968; Brooks & Baddeley, 1976; Cohen & Squire, 1980);

see also Cavaco et al. (2004) for novel experimental tasks based on real-word activities.

We now turn to the implications of our results concerning the issue of determining the extent to which learning was implicit or explicit in this situation.

4.2. Nature of the acquired knowledge: learning without consciousness?

Was learning implicit or explicit in our experimental situation? As discussed in Section 1, generation and recognition tasks allow us to clarify the nature of the knowledge acquired in the SRT task (see Destrebecqz & Cleeremans, 2001; Shanks et al., 2003). Healthy participants trained under deterministic conditions exhibited strong sequence learning during the SRT task, and were also to perform well on the subsequent generation task, successfully reproducing the training sequence under inclusion instructions, and successfully avoiding the reproduction of this sequence under exclusion instructions. The sequential knowledge they have acquired over training thus appears to be explicit. In contrast, healthy participants trained under probabilistic conditions exhibited sequence learning during the SRT task, but were neither able to generate nor to recognize the sequence. This suggests that learning was mostly implicit in this case. The lower complexity and repeating character of the deterministic sequence thus allows participants to acquire conscious, episodic knowledge when trained on such material – knowledge that they can also use directly in a controlled manner. With deterministic material, participants can at best form episodic traces of small fragments of the sequence. Healthy participants trained on a probabilistic sequence, in contrast, exhibit learning over the SRT task yet remain unable to express the acquired knowledge during generation. In addition, even poor-quality traces are capable of influencing processing (indeed, the behaviour of healthy participants exposed to a probabilistic sequence is modified with training, leading the participants to react faster on the elements with a higher probability of occurrence). However, these influences occur only in conjunction with other sources of stimulation, i.e., other cues, such as the presence of more context information, which tightly constrains what response should be made. Such indirect effects are not necessarily accompanied by awareness.

Whether learning was implicit or explicit in amnesic participants is less clear-cut. Though we did observe some learning during the SRT task when the sequence was deterministic, the results of the patient group on the subsequent generation tasks is somewhat difficult to interpret because it might be the case that whatever episodic knowledge had been acquired was by then forgotten. Finally, as amnesic patients trained under probabilistic conditions did not exhibit substantial sequence learning during the SRT task, the issue of the nature of their knowledge is not relevant in their case.

4.3. A multiple learning systems perspective?

Our results are congruent with previous research on amnesia conducted in other fields. Thus, for example, Chun and Phelps (1999) found that amnesic patients were impaired for learning associations between repeated visual configurations and the location of a target. They suggested that amnesia results in a deficit in learning contextual information, which requires the binding of multiple spatial or temporal cues. Another experiment points to the same conclusion. Ryan et al. (2000) examined the performance of amnesic patients using eye movement monitoring to measure memory for spatial relations among objects within scenes. Amnesic patients showed a normal general facilitation when scanning familiar scenes but failed to show excessive scanning of manipulated zones in the rearranged scenes. Again, this suggests that amnesia results in a selective deficit in memory for the relations among the constituent elements of scenes or events.

Our results are consistent with a multiple learning systems view, in which memory for stimulus relationships (“binding”) would be impaired in amnesia and result in their decreased ability to learn about novel information at a normal rate. However, thanks to other hippocampus-independent learning systems, learning would still be possible, particularly when the same contextual information is repeated (that is, without noise). This is the case for procedural learning (Milner et al., 1968; Brooks & Baddeley, 1976; Cohen & Squire, 1980; Cavaco, Anderson, Allen, Castro-Caldas, & Damasio, 2004) in general, and also, we argue, for the deterministic sequences used in this study. Future research will have to explore whether other variables, such as time available for processing, that is, the interval between participants’ responses and the onset of the next stimulus in the SRT task influence the development of episodic representations of the links between the temporal context set by previous elements of the sequence and the location of the next stimulus in amnesic patients.

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