INVOLVEMENT OF THE HIPPOCAMPUS IN IMPLICIT LEARNING OF SUPRA-SPAN SEQUENCES: THE CASE OF SJ

Sylvain Gagnon
University of Ottawa, Canada

Jonathan K. Foster
University of Western Australia and Health Department of Western Australia, Perth, Australia

Josée Turcotte
University of Toronto and Rotman Research Institute, Toronto, Canada

Steven Jongenelis
Sir Charles Gairdner Hospital, Perth, Australia

Learning of supra-span sequences was assessed in a densely amnesic individual (SJ) who suffers from a substantial circumscribed bilateral lesion to the hippocampus. SJ’s ability to lay down information originating from repetitive memory recall episodes was assessed using Hebb’s supra-span procedure. After assessment of short-term memory span, 25 sequences of span +1 items were presented to SJ for immediate serial recall (ISR), one sequence being presented repeatedly eight times. Learning was deduced by the comparison of ISR scores on the repeated versus nonrepeated sequences of span +1 items. SJ’s learning capacity was examined using four different types of stimuli: digits, spatial locations (Corsi block tapping test), words, and pseudowords. Implicit learning of sensorimotor sequences was also assessed in SJ using a serial reaction time (SRT) paradigm. Findings with the supra-span ISR task revealed evidence of learning in SJ with all four types of stimuli. The learning magnitude, as well as learning rate, observed in SJ were comparable to those observed in matched control participants. SJ showed evidence of implicit learning on the SRT paradigm. We conclude that the hippocampus is not required to learn certain types of recurrent information, and that the supra-span ISR task can be considered as an implicit-based learning paradigm. These findings have significant implications for our conceptualisation of implicit learning, and for understanding of the role of the hippocampus in learning.

INTRODUCTION

Since the seminal case of patient HM was reported by Scoville and Milner (1957) in the 1950s, the hippocampus has been strongly associated with the mediation of long-term memory (LTM). However, the specific subtype of LTM that is subserved by the hippocampus remains controversial. One framework that has proven influential distinguishes between “explicit memory,” or...
memory with awareness (which is typically damaged in amnesia, and may be subserved by the hippocampus), and “implicit memory,” or memory without awareness (which is typically preserved in amnesia, and may be independent of the hippocampus; Shimamura, 1986; Squire, 1992).

The present report deals with the effect of hippocampal brain damage on implicit learning of sequences. In an implicit learning task, knowledge is acquired unintentionally as a consequence of experience. The participant is confronted with a task in which various kinds of patterns, associations, or other forms of structure are embedded in the stimuli presented. In the laboratory, implicit learning has been assessed with a number of paradigms, the most popular being serial reaction time and learning of abstract grammars (Berry, 1994; Knowlton & Squire, 1994; Nissen & Bullemer, 1987; A. S. Reber, 1993; Shanks & Johnstone, 1999; Stadler, 1993). For example, in the serial reaction time paradigm, implicit learning of the structural sequence is inferred through faster reaction time. Taken together, extant findings indicate that amnesic patients perform quite well on these implicit learning tasks. Moreover, on many occasions amnesic patients perform within normal limits (Cleeremans, 1993; Knowlton, Ramus, & Squire, 1992; Nissen & Bullemer, 1987; Nissen, Willingham, & Hartman, 1989; but see Channon, Shanks, Johnstone, Vakili, Chin, & Sinclair, 2002, for a discussion). At the neurological level, these tasks appear to be subserved independently of the hippocampus and are instead apparently mediated by the basal ganglia, the cerebellum, and cortical areas involved in the control of movement (for example, Doyon, Owen, Petrides, Sziklas, & Evans, 1996; Ferraro, Balota, & Connor, 1993; Grafton, Hazeltine, & Ivry, 1995; Hazeltine, Grafton, & Ivry, 1997; Rauch et al., 1995; see Curran, 1998, for a review).

However, if we take a closer look at the amnesia literature, it is noticeable that one task involving some form of implicit learning has shown some sensitivity to hippocampal dysfunction. Corsi (1972) observed that unilateral and bilateral lesions of the medial temporal lobes significantly altered learning of supra-span sequences, evaluated using Hebb’s recurring sequence task. In this task, the participant is exposed to a series of supra-span sequences (around 24) in which one embedded sequence is presented on several occasions (specifically, the same sequence is presented eight times, i.e., every three sequences). Each item sequence has to be recalled immediately after presentation by the participant. For this task, in the initial phase of testing, the immediate memory span of the participant is clearly established. Next, the participant is told that longer sequences (immediate memory span +1, or immediate memory span +2 or more items) are going to be presented, and that their task is to recall as many items as possible in the correct order. Implicit learning on this task is denoted by better recall of the embedded recurring item sequence in comparison to the nonrecurring item sequences.

Corsi (1972) administered the Hebb recurring sequence task to left, right, and bilateral medial temporal lobe patients. He employed two forms of the learning task: verbal (digits) and spatial (block tapping) tests. Corsi’s findings indicated that all temporal lobe patients expressed immediate memory span levels that were comparable to normal controls. However, Corsi also noted a double dissociation with respect to impaired learning of the recurring sequence. Right temporal lobe patients showed impaired learning of the recurring sequence on the spatial version of the supra-span task, but demonstrated normal acquisition of the recurring sequence on the digit learning task. In contrast, left temporal lobe patients showed a learning deficit on the supra-span verbal task only. Finally, patient HM, who had sustained a bilateral lesion of the medial temporal lobes, was impaired on both the verbal and spatial supra-span recurring sequences.

Although Corsi’s findings seemed quite clear, other subsequent studies have yielded conflicting results. In a more recent study, Rausch and Ary (1990) failed to replicate the double dissociation previously observed by Corsi with supra-span sequences. Instead, they found that patients with right or left temporal lobe lesions showed relatively intact learning of recurring patterns. As far as other amnesic patients are concerned, it is rather unclear...
from the literature whether these individuals are capable of the same form of implicit learning or not: Baddeley and Warrington (1970) observed learning of the digit version of the Hebb recurrent supra-span task in a small group of amnesics (mainly Korsakoff patients), whereas Charness, Milberg, and Alexander (1988) found that their Korsakoff patient could not learn the spatial version of the supra-span task. However, in another study, Milberg, Alexander, Charness, and McGlinchey-Barroth (1988) obtained some signs of learning on this task in one of two amnesic patients who suffered rupture of an anterior communicating artery aneurysm (ACoAA). Moreover, as is often the case in studies of amnesia, the amnesic patients tested in the aforementioned studies had typically suffered brain damage that extended beyond the hippocampal area, or may not have been included the hippocampus per se (for example, in the case of Korsakoff’s or ACoAA patients).

As it stands, the issue of whether or not the hippocampus is critically involved in this type of Hebbian supra-span implicit learning therefore remains unresolved. Moreover, based on the available literature, it is problematic whether or not to classify Hebb’s recurrent digit span task as a truly implicit memory task. According to Seger (1994), one of the criteria that could be used to discriminate implicit from explicit memory tasks is the fact that implicit memory should rest on neuronal systems that exclude the hippocampal system. However, Seger also mentions that this criterion cannot perhaps be applied unequivocally, since Corsi’s original findings with the Hebb supra-span learning task in temporal lobe amnesic patients suggest that, by this criterion, this is not an implicit memory task. Two possible conclusions could be drawn. First, because some temporal lobe patients have learned the supra-span task successfully, but other amnesic patients have shown impairments on the task, it could be argued that brain structures other than the hippocampus may also have been damaged in amnesic patients who failed to show improvements with recurring sequences on Hebb’s task. Second, in terms of a psychological account of the phenomena, one could conclude that this form of supra-span learning is based on the use of explicit strategies, and will only occur if declarative memory processes are intact or partly spared.

The purpose of this study is to disentangle this issue via a thorough evaluation of residual supra-span learning capacities of an amnesic patient SJ, who has sustained neurological damage restricted to a circumscribed region of the medial temporal region which is focused on the hippocampus. Because it has been previously demonstrated that motor sequence learning is usually not impaired in amnesic patients (for example, Doyon et al., 1996; Ferraro et al., 1993; Grafton et al., 1995; Hazeltine et al., 1997; Rauch et al., 1995; but see Curran, 1997), for purposes of reference and comparison we also administered a serial reaction time (SRT) task to SJ. Unlike Hebb’s supra-span learning task, the SRT task does not rely on immediate recall of presented items: The participant’s task is simply to react as quickly as possible to one of four stimuli that are presented in a recurring sequence on a computer screen by pressing the corresponding key. Learning on the SRT task is inferred from faster reaction times to the recurring sequence of stimuli in comparison to randomised sequences of items.

**METHOD**

**SJ**

SJ was 48 years old at the time of experimental testing and was seen over a period of 3 weeks, 13 months after his original injury. SJ has received 18 years of formal education and has enjoyed considerable academic success over his lifetime, working as a well-respected local professional. SJ’s neurological injury appears to be related to a treatment provided in 1999, to relieve symptoms associated with a lower back injury through a lumbar steroid injection. Although there is some uncertainty regarding the precise aetiology of SJ’s amnesia, it seems most likely that this lumbar procedure introduced staphylococcus bacteria into the epidural space, and that this infection was subsequently transmitted to the brain. At the time of the event, SJ was admitted to hospital and
experienced an acute hyperglycaemic event and tonic clonic seizures.

Upon initial admission to hospital, SJ had a Glasgow Coma Scale score of 3. He remained confused and disinhibited for a period of 8 days. He was seen for formal psychometric evaluation 5 months post ictus and was administered a modified short form of the Wechsler Adult Intelligence Scale-Revised (WAIS-R), the Wechsler Memory Scale (WMS), and a range of common tests for the assessment of neuropsychological function. The test results showed preserved general intellectual function with prorated (Ward’s Transformation) Verbal, Performance, and Full Scale IQ scores in the “superior” range (prorated scores of 123, 124, and 127, respectively). At this time, SJ was also administered the following tests: Rey Complex Figure (copy and incidental recall), Controlled Oral Word Association Test (FAS) and Austin Maze Learning. Psychometric assessment at this time showed that SJ’s memory was severely impaired and significantly below expectations. His memory performance was characterised by an extremely rapid rate of forgetting; for example, on the Rey figure his copy score was at the 100th percentile, while his reproduction score was at the 1st percentile. Examination of the psychometric test profile with regard to executive functions did not suggest impairment in this domain.

A cranial MRI was undertaken 7 months after the time of the injury. This revealed increased signal within the mesial temporal lobes bilaterally. The abnormal signal involved both amygdala and hippocampi (the head and tail of the hippocampal gyri were involved). The coronal images suggested slight loss of volume of the hippocampal gyri bilaterally. No other atrophic neural changes were detected (see Figure 1).

Follow-up neuropsychological examination was undertaken 18 months after SJ’s initial hospitalisation. On this occasion, the test battery included the Wechsler Adult Intelligence Scale III (WAIS-III) and the Wechsler Memory Scale III (WMS-III). At this time, SJ was also administered the following tests: Rey Complex Figure (copy and incidental recall), Controlled Oral Word Association Test (FAS), Symbol Digit Modalities, Trail Making,

Figure 1. Structural MRI scan (coronal view) of SJ’s lesion.
(4 SDs below the mean). On recognition, SJ produced a discriminability score of 63.6 (≈ 4 SDs below the mean) and a bias score of 0.75 (approx. 2.5 SDs above the mean). Of note, on recognition SJ identified 14/16 target items correctly, but he also produced 14 false positive responses to foil items. On the Rey figure, SJ again showed evidence of fast forgetting, scoring at the 70th percentile on copy (34/36) but scoring zero on reproduction of the figure. On this second occasion of psychometric evaluation, there was again no sign of executive dysfunction in SJ.

Control participants

Twelve participants 11 males and 1 female, were recruited. On average, these participants had 18.16 (±0.12) years of formal education and were 46.75 years old (±2.6) at time of testing. A female was included in our sample because of the difficulty of finding an additional male participant sharing a similar demographic profile as SJ. All control participants originated from the Toronto metropolitan area in Canada.

Material

For SJ, all stimuli were presented on a 14-inch screen Fujitsu laptop PC equipped with a 450 MHz Celeron processor. A total of 4 supra-span tasks were used (digits, words, pseudowords, and spatial positions). For the control participants, stimuli were presented on either a 17-inch Mitsubishi screen or a 15-inch Micro Scan screen. The PCs were respectively equipped with a Pentium 133 MHz or 486 MHz processor. All tasks were computerised and programming was undertaken using the MEL II Professional Edition. Digits from 1 to 9 were used in the immediate memory span estimation task, as well as in the digit version of the supra-span learning task. Both words and pseudowords were carefully selected, based on Hulme, Maughan, and Brown's (1991) study. The nine words used were periodical, aluminium, Yugoslavia, physiology, tuberculosis, accommodation, hippopotamus, refrigerator, and university. The pseudowords were zegglepim, gossikos, tushebon, teggidbim, muttasek, jodazum, giffoldof, greluppid, and monoisip. In the spatial version of Hebb’s task, 12 two-dimensional 225 mm² squares were irregularly positioned on the computer screen. The display of the squares was inspired by the display used by Corsi (1972). The squares were dark grey and appeared on a light grey background. In the span task, 16 sequences were randomly generated for each type of material, whereas in the supra-span task, 17 sequences were needed. The repeated sequences used in the supra-span tasks were the same for JS and control participants. The repeated sequences were as follows: digits, 3 7 4 6 2 8 5 9 1 6 4 8; words, refrigerator–accommodation–Yugoslavia–aluminium–periodical–university–hippopotamus–physiology–tuberculosis; pseudowords, gossikos–muttasek–zegglepim–monoisip–greluppid–tushebon–teggidbim–giffoldof–jodazum. For an illustration of the repeated sequence used in the spatial condition, see Figure 2.

The display for the SRT task consisted of four white 225 mm² horizontally aligned squares located in the centre of the computer screen. The distances between each of the successive squares was 55 mm. Squares were aligned to one of X, V, M, and . keys on the keyboard below. A square piece of blue paper was tagged to each of these keys, for the benefit of the participants. A solid blue line appearing in the middle of the designated white square on the computer screen was used as the signal, and the
appropriate response was for the participant to press the corresponding computer key (i.e., X, V, M, or .) as soon as possible. The repeated pattern consisted of the following sequence of 10 items: 4, 2, 3, 1, 3, 2, 4, 3, 2, 1 (the numbers designate the spatial position of the squares on the monitor, reading from left to right).

Procedure
SJ was seen on four occasions, twice per week during two consecutive weeks. Each testing session lasted between 60 and 90 minutes. In session 1, the spatial version of the span and supra-span learning task was administered. In session 2, SJ’s sequence learning capacity was assessed further using digits. In session 3, the SRT task was administered followed by the word version of the task. Finally, in session 4, digit supra-span learning was reassessed together with the pseudoword version of the task. Therefore, in each session, the span and the supra-span learning of one type of stimulus was assessed. The digit supra-span was administered twice (sessions 2 and 4) because SJ’s immediate serial recall (ISR) quickly reached ceiling on recall of the nonrecurring sequences on Session 2. In session 4, the list length corresponded to span +2 items. After each supra-span task, SJ was administered two questions: (1) “did you notice anything peculiar about the task?” and (2) if and when SJ said that some sequences seemed more familiar to him than others, or that there was some form of repetition in the task, SJ was requested to recall the repeated information.

In control participants, testing was completed in one session that lasted approximately 60 minutes. Both the span and the supra-span learning tasks were administered within the same testing session for the four different types of test materials (i.e., digits, blocks, words, pseudowords and spatial locations) used in this study.

Hebb supra-span learning task
Twenty-five sequences of span +1 items were presented to patient SJ and to 10 out of the 12 control participants. Two of the control participants tested in the digit condition were instead given span +2 or span +3 items because they developed strategies during the course of their span estimation that increased their span dramatically. This was noticed at the end of the span estimation task. The supra-span list length was therefore increased accordingly for these two participants. The recurrent sequence was administered eight times; that is, on trials 3, 6, 9, 12, 15, 18, 21, and 24. Within each sequence of the spatial condition, item duration was 1250 ms followed by an inter-item interval of 250 ms, whereas in the verbal conditions (digits, words, and pseudowords), item duration was 1800 ms followed by an inter-item interval of 750 ms. In all conditions, presentation rate was slow enough to allow adequate processing of all the items by each participant tested. After the last item of each sequence has been presented in the verbal conditions, a visual cue “!!!” prompted the participant to start recalling all of the items presented in the previous sequence, in the appropriate order. In the spatial condition of the supra-span learning task, the prompt recall was indicated by a brief change of the blocks’ colour, which temporarily turned white. When the colour of the squares turned back to grey, the participants had to reproduce the sequence by pointing to the squares with his finger in the appropriate order. In all conditions,
if the participant could not remember one item of the sequence, he or she was told to say “blank” and continue with the remainder of the sequence. Twenty seconds was allowed to recall all of the items, after which the presentation of the next sequence appeared on the screen.

**Serial reaction time task (SRT)**

The SRT task was only administered to SJ, for purposes of comparison with performance on the Hebb supra-span task. SJ was told to react as quickly as possible to the blue line appearing in one of the squares on the computer screen by pressing the corresponding marked blue key on the keyboard, at the same time maintaining a high level of accuracy. The computer response keys were activated by SJ using the left middle, left index, right index, and right middle fingers placed on the marked blue keys (i.e., keys X, V, M or .). The computer timer started at the onset of the stimulus and stopped in response to each of SJ’s key-strokes. The task comprised nine blocks of 100 trials each. The first two blocks provided randomised trials. Feedback for incorrect responses was given in the first block only. In the next five blocks (i.e., blocks 3–7 inclusive), the same sequence of 10 items was continuously presented. Therefore, the repeated sequence was presented 10 times in each of these five blocks. In block 8, the sequence reverted to randomised trials, and this was followed in block 9 by the presentation of the repeated sequence again.

**RESULTS**

**Supra-span results**

SJ’s span was estimated as being 8 for digits, 6 for spatial positions, 4 for words, and 3 for pseudowords. SJ’s span scores were quite similar to the scores obtained on average by control participants (digits = 9, spatial positions = 6.6, words = 3.3, and pseudowords = 2.9). Lower spans observed in the word and pseudoword conditions can be explained by the number of syllables of the words coupled with the inherent lack of familiarity of the participants (including SJ) with the pseudowords.

In order to determine whether SJ and control participants showed implicit learning in the supra-span task, a global analysis was performed in which recall of repeated and randomised sequences was compared. SJ’s and the control participants’ learning performance were examined separately. In the case of SJ, each data entry corresponded to the level of recall of the repeated sequence and to an average of the randomised sequences that preceded and followed the repeated sequences. Trials 1 to 4 are considered as a baseline, and were therefore not included in the following analysis. Consequently, there were 14 data points for each test: 7 repeated sequences (sequence 6, 9, 12, 15, 18, 21, and 24) and 7 comparable scores for the other randomised sequences. However, it should be noted that for the word supra-span condition, sequences 23 to 25 of the test session were eliminated because SJ clearly expressed verbally that he felt tired and could pay no further attention to the sequences at all. When this happened, SJ was told to do his best, because the computer program could not be stopped at that point. For these three trials (i.e., trials 23–25 of the word task), SJ declined to recall the words, claiming that he was too tired. For this reason, only 12 data points were considered for the global analysis of the word task in SJ.

Overall, across all four tasks, SJ correctly recalled 79% ($SD = 27$) of the items of the repeated sequences whereas only 56% ($SD = 25$) of the items of the randomised sequences were correctly recalled (see Table 1). A $t$-test on SJ’s recall scores indicated that the difference between his correct performance on the repeated and randomised trials was statistically significant, $t(54) = 3.56, p < .01$. It therefore seems that, despite his brain injury, SJ demonstrated the capacity of learning the repeated item sequences on the supra-span task.

In control participants, overall learning was again examined by comparing the combined performance of all 12 participants on repeated and non-repeated sequences. On average, in controls immediate recall of repeated sequences reached 75% ($SD = 18.2$) and 61.5% on non-repeated sequences ($SD = 17.7$). A $t$-test confirmed that this difference was highly significant, $t(11) = 5.07, p < .001$. 

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In the second set of analyses, we examined whether SJ’s acquisition of the supra-span sequence generalised across each of the four test conditions (i.e., digits, words, pseudo-words, spatial positions). Inspection of Figure 3 indicates that SJ learned the repeated sequence in all four conditions (i.e., spatial locations, digits, words, and pseudo-words): In all four conditions, there was a cumulative increase in SJ’s performance from the 1st occurrence of the repeated sequence onwards.

To examine further SJ’s performance statistically, the significance of the linear regression lines for repeated and randomised sequences was computed. These are summarised in Table 2. Immediate serial recall (ISR) scores were predicted using block number. For each regression analysis, eight data points were entered. For reasons already mentioned, only seven data points were used in the word condition. These analyses confirmed that, in the spatial, word, and digit conditions, the regression lines for the randomised sequences were flat and the slope coefficient did not reach significance. By contrast, the regression lines for the repeated sequence were positive and the coefficient did reach significance. The analysis of the repeated items did not yield statistically significant results for the digit and Corsi (i.e., spatial blocks) conditions. However, inspection of the regression lines provides a possible explanation for this. In the digit condition, immediate serial recall quickly reached ceiling (first repetition) for the repeated sequences and remained at that level. A similar interpretation also applies to SJ’s results in the Corsi condition. In this condition, there was evidence of learning for the repeated trials, but near-ceiling performance on blocks 3 to 8 and very low performance on the first repetition of the sequence eliminated the possibility of a significant regression line. One should also keep in mind that the statistical power of each analysis was relatively low because of the limited number of data points. Another indication of the presence of learning is the fact that no apparent proactive interference or fatigue was observed on the ISR of the repeated sequence (Heron & Craik, 1964). In contrast, in the word, spatial, and digit conditions, ISR for the randomised sequences seemed to decline in the later stages of testing.

A different pattern of results was obtained in the pseudoword condition, where learning was, unexpectedly, observed for both repeated and

| Table 1. Average recall score (mean ± SD) of SJ and control participants on repeated and randomised sequences in the four supra-span conditions |
|---------------------------------|-----------------|-----------------|-------------------|-----------------|
| Condition                      | Repeated sequences | Randomised sequences |
|                                | SJ               | Controls         | SJ               | Controls         |
| Digits                         | .89 ± .29        | .91 ± .07        | .60 ± .28        | .83 ± .06        |
| Corsi                          | .88 ± .17        | .77 ± .09        | .76 ± .07        | .61 ± .13        |
| Words                          | .77 ± .33        | .84 ± .12        | .42 ± .17        | .61 ± .17        |
| Pseudowords                    | .61 ± .29        | .60 ± .11        | .33 ± .22        | .38 ± .06        |
| Total                          | .79 ± .27        | .75 ± .18        | .56 ± .25        | .62 ± .18        |

| Table 2. Linear regression analyses (recall scores as a function of block of trials) for repeated and randomised sequences of each supra-span learning task of SJ |
|---------------------------------|-----------------|----------------|
|                                | MS              | F<sup>a</sup>  | p               |
| Digits                         |                |                |
| Repeated                       | 0.200           | 3.000          | .13             |
| Randomised                     | 0.001           | 0.017          | .90             |
| Corsi                          |                |                |
| Repeated                       | 0.230           | 2.289          | .18             |
| Randomised                     | 0.017           | 0.665          | .45             |
| Words                          |                |                |
| Repeated                       | 0.210           | 13.500         | .01             |
| Randomised                     | 0.060           | 3.000          | .14             |
| Pseudowords                    |                |                |
| Repeated                       | 0.340           | 9.070          | .02             |
| Randomised                     | 0.170           | 6.400          | .04             |

<sup>a</sup> All df = 1.
nonrepeated sequences in SJ. The coefficient of regression for SJ reached significance for both randomised and repeated sequences in the pseudoword task. The occurrence of learning in the randomised sequences of pseudo-words may reflect the initial lack of familiarity with the stimulus materials. Gagnon, Poirier, and Turcotte (1997) have, in fact, observed a similar finding in young healthy adults. From trial to trial, SJ’s fluency to pronounce the pseudowords increased, as one might expect. This effect probably mediated the apparent learning that was observed in SJ for both repeated and nonrepeated pseudowords.

A similar set of analyses was applied to control participants for each one of the supra-span tasks (see Table 3 and Figure 4). For the purpose of comparability, the analyses were identical to the analyses performed on SJ’s scores. The analyses revealed that all regression analyses applied to the repeated sequence reached significance in controls. In contrast, none of the regression analyses performed on nonrepeated sequences reached statistical significance in controls. Moreover, it is interesting to note that the magnitude of the regression coefficients associated with repeated sequences were similar or smaller in control participants in comparison to SJ. This last result indicates that the rate of learning for the repeated supra-span sequences was normal in SJ.

The previous analyses provide a good indication that learning did in fact occur for SJ on the Hebb supra-span learning task. We especially highlight the fact that SJ’s overall level of recall for the repeated sequences was higher than his immediate recall of the randomised sequences in all four conditions (see Table 1). Similar findings were also obtained in control participants.

The nature of SJ’s answers to the questions asked of him after each supra-span tasks indicates that his learning was probably implicit. On one occasion, SJ told the experimenter that he did not notice anything about the task (i.e., spatial blocks condition), and when probed about the repeated sequence, perhaps not surprisingly, SJ, said that he could not recall any items of the sequence. By comparison, in the digit, word, and pseudoword conditions, SJ said that some sequences seemed to have been remembered even though he was not aware of having done so.

Figure 3. SJ’s learning curves and regression lines for the recurrent and randomised sequences in the digit (a), spatial (b), pseudoword (c), and word (d) conditions.
more familiar to him than others. However, when asked to recall the familiar items, SJ said that it was impossible for him to reproduce any of them.

**Serial reaction time results**

SJ's learning curve on the SRT task is depicted in Figure 5. Trials were eliminated from the following analyses if an error was made (i.e., the wrong key was pressed), if the reaction time was 3 SDs slower than the mean reaction time for a session, or when the reaction time was faster than 150 ms. It is clear that SJ learned the repeating serial pattern, as his reaction time decreased steadily from session 3 to session 7. When confronted with a randomised sequence on session 8, SJ's reaction time increased, indicating that learning on sessions 3 to 7 was mainly caused by the repetition of the sequence. Finally, in session 9, SJ's reaction time decreased again when the repeated pattern was reintroduced.

A series of *t*-test analyses were performed to examine the previous observations. Each reaction time was considered as an independent observation. The analyses revealed that reaction time on session 7 was quicker than on session 3 by 117 ms, *t*(99) = 6.33, *p* < .001, showing that significant learning did occur across these sessions. The introduction of randomised sequences in session 8 slowed down
reaction time significantly in comparison to session 7 (101 ms), \( t(99) = -6.66, p > .0001 \). Finally, as depicted in Figure 5, serial reaction time decreased significantly again in session 9 compared with both session 8 (135 ms), \( t(99) = 8.7, p < .0001 \), and session 7 (35 ms), \( t(99) = 2.74, p < .05 \). Quite surprisingly, we observed a sudden decrease of reaction time in session 3 (i.e., the first trial of the repeated sequence) in comparison to session 2 (101 ms), \( t(99) = 6.23, p > .001 \). There are at least two possible reasons for this significant and sudden decrease: SJ learned the repeated sequence quite rapidly, or the elements of the repeated sequence were easier to react to than the elements of the previous randomised sequences. It appears that both reasons may provide a partial explanation for this decrease in response time in session 3. Note that the reaction time of the first 50 trials of session 3 was 60 ms faster than the last 50 trials of session 2. However, we did additionally observe a significant decrease in reaction time in SJ within session 3 of the SRT task: the average reaction time over the last 50 trials of session 3 was 469 ms (\( SD = 155 \)), in comparison to 526 ms (\( SD = 152 \)) in the first 50 trials of session 3. Therefore, although the repeated serial sequence that we used to examine learning across sessions 3–7 may be considered relatively straightforward to perform, specific learning did occur within session 3 and, subsequently, on sessions 4–7.

**DISCUSSION**

The results of the present study demonstrate quite convincingly that the hippocampus has a limited role with respect to implicit learning of recurrent sequences. SJ, a densely amnesic individual suffering from bilateral damage to the hippocampus, demonstrated learning of a recurrent sequence in four different conditions of the Hebb supra-span learning test. In addition, as previously observed by other researchers who have investigated the performance of amnesic participants (Nissen & Bullemer, 1987; Nissen et al., 1989; P. J. Reber & Squire, 1994, 1998), SJ’s reaction time decreased linearly in the SRT paradigm. The findings on the SRT task provide additional evidence that processes underlying implicit learning are spared in amnesic individuals who have sustained selective hippocampal damage.

In this report, we provide the first empirical demonstration that a densely amnesic patient can show learning of a repeated sequence based on immediate serial recall. Increased immediate serial recall of the repeated sequences in comparison to the random sequences in SJ was similar to what we observed in the control participants that we also tested. Furthermore, this is the first experiment in which an amnesic patient was assessed on several different versions of the Hebb supra-span task, allowing us to assess whether any deficits present
were stimulus-bound or not. Our observations revealed that learning of a supra-span sequence did not vary substantially in SJ from one task to another, whether the sequence included a motor response (i.e., spatial condition) or not, or whether the stimuli were familiar (words) or not (pseudowords). By the same token, testing the patient in four different supra-span conditions, as conducted in this study, increases the validity of our observations. As the various analyses indicated, SJ demonstrated an impressive level of learning on all four supra-span tasks. In fact, SJ demonstrated a learning rate that was comparable to age-matched control participants in all four supra-span tasks. However, because each task was administered only once, there is some obvious noise in SJ’s data (compared with the control data, where the findings were averaged across 12 participants), and some learning curves do not follow a cumulative pattern. This is especially true for the data from digit and pseudoword conditions in SJ. In one case (i.e., digits), SJ’s performance on the recurrent sequences reached ceiling very early on, whereas in the other condition (pseudowords) learning apparently occurred in SJ for both recurrent and random sequences. In the case of digits, the early ceiling effect does not detract from the relevance of the data, since SJ’s performance on the random sequences was lower overall. (One should also note that very high ISR performance was also noticed early on in control participants in the digit condition. For SJ and two controls, the list length had to be increased in order to obtain a valid assessment of supra-span learning.) In the pseudoword condition, apparent learning in SJ occurred with both types of sequences, but this appeared stronger with the recurrent sequence. (As previously mentioned, in control participants the learning rate for the repeated sequence of pseudowords was comparable to that observed in SJ, but the learning rate did reach statistical significance for the controls because of greater statistical power.)

Overall, our data provide compelling evidence that SJ, despite his profound amnesia, demonstrates substantial learning of a recurrent sequence of items through ISR. By contrast, in other studies evaluating amnesic patients (Corsi, 1972; Milner, 1971), supra-span learning was almost at floor levels. Our findings offer a response to Seger (1994), and confirm that learning of supra-span sequences does not rest on or require long-term explicit memory mechanisms.

Our study also differs from previous reports (Corsi, 1972; Milner, 1971) in which learning was deduced from the proportion of sequences correctly recalled as a whole. Instead, in this study we decided to examine item and order information more precisely, i.e., for each element of the sequences (McKelvie, 1987). The advantage of our scoring method is its sensitivity, in that even partial learning of a sequence may be considered to be a significant performance increment. Our scoring method also allowed us to plot SJ’s scores according to the number of repetitions of the sequence, and to illustrate with increased precision the presence or absence of learning. Using this method, we were able to demonstrate that learning did in fact take place in SJ, and that for most conditions it was built up from trial to trial. In previous studies conducted by other researchers, this scoring method was not applied, and it is therefore difficult to determine whether the conclusion of “no learning” in previously tested amnesic patients was appropriate or not. This is a very important issue considering that in the present experiment we showed that, overall, learning was significant in the word condition, even though only one repeated sequence was recalled correctly as a whole. Indeed, the subsequent regression analysis revealed that the linear trend was significant for the word condition, illustrating significant learning. In this sense, our data strongly suggest that the individual item scoring method that we used is more meaningful than other statistical approaches. Clearly, in conditions where recall of the entire sequences was frequently observed by participants (e.g., digits or spatial positions, in this study), one would definitely expect that an analysis based on item and order would yield similar findings compared with an analysis based on the frequency of correctly recalled sequences. By comparison, the item and order analysis used here appears extremely valuable when subjects are in fact unable to recall a complete sequence, but where some of the items are recalled correctly. We
therefore suggest that the type of analysis used in this study is employed when evaluating ISR data before concluding that this form of learning is impaired.

Our present results contrast with the findings of previous reports indicating that amnesic patients with hippocampal damage show relatively little learning of repeated sequences in Hebb supra-span type tasks (Baddeley & Warrington, 1970; Charness et al., 1988; Drachman & Arbit, 1966; Milberg et al., 1988; Milner, 1971). In his set of experiments, Corsi (1972) observed a double disso-ciation between the nature of the task and the hemispheric side of the patients' medial temporal lobe resection. Corsi's original observations suggested that the memory processes involved in the supra-span task were lateralised according to the nature of the stimuli: Corsi reported that right temporal lobe patients were significantly impaired on the spatial version of the supra-span task whereas left temporal lobe patients had difficulty learning the repeating sequence when digits were used. Moreover, Corsi observed that the learning deficit was much more striking with patients whose temporal lobe resection included a larger portion of the hippocampus. For this reason, at the time of Corsi's original study it was concluded that the hippocampus is a significant mediator of the development of memory traces laid down by repetition through immediate serial recall. However, Rausch and Ary (1990) could not replicate Corsi's finding, and these authors therefore concluded that deficits on supra-span learning do not correlate with the involvement of the hippocampus.

As we described previously, SJ suffered from significant bilateral damage to the hippocampus and, for that reason, according to the previous findings of Corsi (1972), he should not have been able to learn any of the supra-span tasks that we used in this study. However, we report quite the opposite finding here. We believe that as well as differences resulting from the scoring method used here, the main reason why learning did occur in SJ relies on the fact that the type of implicit learning we studied here does not, in fact, rely on the integrity of the hippocampus. This was also revealed by SJ's normal performance on the SRT task, another implicit learning paradigm (in which the scoring procedure that we used was the same as that used in many previous studies). The extent of the hippocampal lesion, in association with the nature of the memory impairment, is a very important issue that needs to be considered in order to interpret the severity of memory deficits in amnesic patients (Gabrieli, 1998). Rausch and Ary (1990) suggested that a lesion of the area neighbouring the medial temporal lobe, such as the superior temporal gyrus, in combination with resection of the hippocampus, could result in implicit learning impairment in tasks such as the supra-span task. Although the brain circuitry underlying implicit learning is not fully known, this interpretation is certainly possible, and suggests that, considered independently, the hippocampus does not directly mediate implicit learning. However, in combination with damage to additional brain structures, implicit learning deficits may indeed occur in "hippocampal" patients. It is very important to highlight the fact that none of the amnesic patients tested previously on supra-span tasks had a lesion that was restricted to the hippocampus, as is the case for patient SJ. Moreover, a recent brain-imaging study performed by Schendan and Kutas (2003) has revealed that the hippocampus and related cortices were likely to be involved in processing of higher-order associations in sequence learning (see also Curran, 1997).

Another issue that we wish to address in this paper concerns the implicit nature of Hebb's supra-span task. Hebb's task is peculiar because of its reliance on explicit immediate recall. In many, if not most implicit memory tasks, participants do not have to execute any form of recall. This raises the possibility that learning in Hebb's supra-span task may in fact be mediated by explicit recall strategies (Stadler, 1993). Proposing that the task is implicit because SJ did show significant learning would then be considered circular. However, in the post-task interview, SJ stated on one occasion (i.e., for the Corsi task) that he did not notice any recurrence of information. This raises the possibility that learning in Hebb’s supra-span task may in fact be mediated by explicit recall strategies (Stadler, 1993). Proposing that the task is implicit because SJ did show significant learning would then be considered circular. However, in the post-task interview, SJ stated on one occasion (i.e., for the Corsi task) that he did not notice any recurrence of information. This raises the possibility that learning in Hebb’s supra-span task may in fact be mediated by explicit recall strategies (Stadler, 1993). Proposing that the task is implicit because SJ did show significant learning would then be considered circular. However, in the post-task interview, SJ stated on one occasion (i.e., for the Corsi task) that he did not notice any recurrence of information. This raises the possibility that learning in Hebb’s supra-span task may in fact be mediated by explicit recall strategies (Stadler, 1993).
during the ongoing supra-span task. Unfortunately, these observations only provide a partial answer to the issue of possible explicit processing in SJ on the Hebb supra-span task. These observations are nevertheless in agreement with McKelvie’s (1987) findings in control participants, which clearly indicate that learning of the repeated sequence cannot be predicted by awareness of the recurrent sequence. Because it is partly based on explicit short-term recall, the Hebb supra-span task might induce a high feeling of familiarity, which can result in full consciousness of the repeated sequence in normal participants. By contrast, having corroborated the extensive nature of SJ’s long-term explicit memory deficits through standardised neuropsychological investigation, it is quite unlikely that SJ’s ability to learn the repeated sequence was even partly based on his explicit knowledge of the sequence.

This brings us to the question of whether the hippocampus is mainly involved in the mediation of conscious (i.e., explicit) forms of learning and memory. Although this issue is partly beyond the scope of this paper, we do believe that our findings provide evidence that learning should develop normally in amnesic individuals with lesions restricted to the hippocampus, when these learning tasks require the involvement of memory processes that rest in brain circuitry that is spared or partly spared in amnesic individuals. Interestingly, performance on the Hebb supra-span learning task is based on intact ISR processes, as well as the appropriate nonconscious build-up of long-term memory traces. Assessment of span in all four tasks indicated that SJ’s short-term recall was comparable to that of our control participants. Moreover, his performance on the SRT task revealed that his capacity to acquire information based on repetition (but not awareness) was also spared. When we bring together these observations, the demonstration that SJ performed within the normal range on the Hebb supra-span learning task is consistent with SJ’s preserved cognitive abilities. Only one aspect of SJ’s experience with the recurrent information seems to be impaired; that is, his ability to generate appropriate recall strategies in order to retrieve information about the repeated sequence. In other words, learning of the type assessed by the recurrent supra-span task is possible following amnesia, but this learning can only be accessed indirectly (i.e., through steady ISR increments). Other researchers have argued that the effect of amnesia on memory is best explained by a reduced learning rate in one memory system, rather than by the existence of different memory systems based on conscious versus unconscious processing (Kinder & Shanks, 2001). These researchers suggest that, in situations where the learning rate is slower in amnesic individuals (e.g., when the stimulus material is not familiar, see Gooding, Mayes, & Van Eijk, 2000), impairment even in implicit learning tasks will be observed. According to Kinder and Shanks, a one-system approach to memory functioning is not only more parsimonious, it also resolves some of the discrepancies noted in the literature regarding the effects of amnesia on implicit learning tasks (Chun & Phelps, 1999; Curran, 1997; Knowlton et al., 1992; Nissen & Bullemer, 1987). In contrast, our data suggest that SJ was able to learn the supra-span task at a level comparable to control participants, even when the sequences were composed of low-familiarity items (pseudowords). Single process models may be able to provide an account of much of the memory literature with respect to the manipulation of only one parameter (such as learning rate), as stated by P. J. Reber (2002). Nevertheless, they fail to demonstrate one important characteristic of explicit memory processes; that is, the observed capacity to retrieve some information after only one exposure (i.e., one-trial learning). Considering that SJ apparently had no conscious access (during the post-task interview) to repeated sequences for which his ISR was perfect after a number of repetitions (i.e., digit and spatial conditions), we believe that the hippocampus plays a central function in mediating long-term explicit memory processes. When our findings here are considered in conjunction with the wider amnesia literature, it would seem likely that only when tasks are based on spared nonaware processes will performance (e.g., implicit learning or ISR) reach control levels.

In conclusion, in this study we observed that SJ was able to learn recurrent sequences comprising...
various different experimental stimuli. SJ's learning did not seem to vary qualitatively according to the nature of stimuli, and his learning was observed whether task responses had to be produced verbally or manually. Learning of repeated sequences was also observed in SJ on an implicit serial reaction time task. We conclude that learning of verbal and nonverbal supra-span sequences does not rely on the integrity of the hippocampus. These findings have important implications, not only for our understanding of the neural basis of different forms of memory, but also in terms of possible rehabilitation strategies useful for patients with selective hippocampal damage.

REFERENCES


