Published in final edited form as:

Behav Brain Res. 2010 April 2; 208(2): 576–583. doi:10.1016/j.bbr.2010.01.002.

Individual Differences in Face Recognition Memory: Comparison among Habitual Short, Average, and Long Sleepers

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Abstract

Research indicates that habitual short sleepers show more rapid accumulation of slow-wave sleep at the beginning of the night. Enhancement in performance on declarative memory tasks has been associated with early NonREM sleep, consisting of the highest percentage of slow-wave sleep. Twenty-four subjects (8 short sleepers 7 hrs, 9 average >7 but <9 hrs, 7 long 9hrs) were tested. Subjects were presented with unfamiliar face stimuli and asked to memorize them for a subsequent test. Following sleep, the subjects were presented with the 40 “old/studied” items intermixed with 40 new and asked to indicate the previously presented stimuli. Event-related potentials (ERPs) were analyzed to verify the existence of the “Old/New” effect, i.e. amplitude difference [in ERPs] between the old and new stimuli. ANOVA on the scores revealed a significant interaction between the stimuli and group. Post-hoc test on the studied items revealed more accurate responses in the short sleepers compared to the average and long sleepers. Strikingly, the long sleepers, failed to show significant retention of the old/studied items, with their recognition of old faces not different from chance. RT responses were faster for the old versus the new items. Pearson correlation revealed a significant negative correlation between accuracy and sleep duration in the short sleepers. However, long and average sleepers showed a positive correlation between the two variables. ANOVA performed on the ERPs revealed main effects of stimuli and site, and no interactions involving the group factor. In conclusion, our data show that individual differences in recognition memory performance may be associated with differences in habitual sleep duration.

Keywords

Cognitive event-Related Potential; ERPs; N400-P600; recognition memory; sleep; individual differences

Introduction

Individual differences in sleep in healthy adults have been investigated for several decades. According to recent polls, the average adult sleep duration is ~8 hours per night [45] and a standard deviation of approximately 1 hour has been reported [73]. The basis of this variation is unknown. Even with less restricted sleep schedules and longer sleep opportunities, this 1-hour standard deviation still persists. Individuals generally sleep more on weekends [45], but even when considering these less restrictive conditions, the standard deviation is about the same as on weekdays [45]. In a study in which young, healthy adults were given 14-hour sleep opportunities for a four-week period, the average sleep duration was 8.2 hours per night and the standard deviation was still 1.1 hour [75]. Together, these data suggest that endogenous influences contribute to differences in sleep duration.

Several electrophysiological studies on individual differences in sleep duration have reported differences in sleep structure and sleep/wake variables [11; 31; 74]. Early studies showed that habitual short sleepers experienced less total sleep time, decreased rapid-eye-movement (REM) sleep and light sleep, but similar amounts of slow-wave sleep (SWS) compared to habitual long sleepers [74; 11; 31]. Because SWS is a deeper form of NonREM sleep, the results were interpreted to mean that short sleepers have a “more efficient sleep pattern” [74]. When comparing short and long sleepers based on the longest common sleep interval of slightly less than 5 hours, Aeschbach *et al.* reported that short sleepers showed a *relative increase* in the amount of SWS and less light sleep than the long sleepers [1]. Later, it was reported that in short sleepers there was a rapid accumulation of SWS at the beginning of the night [4]. The shorter sleep latency and the more rapid accumulation of SWS in the short sleepers was interpreted as a consequence of higher (homeostatic) sleep pressure at the beginning of the night [2]. In concordance with these findings, evidence for a group difference in the tolerance to high sleep pressure comes from another sleep deprivation study, in which short and long sleepers rated their sleepiness on the Stanford Sleepiness Scale during ~40 hours of wakefulness. During wake extension beyond ~30 hours, the short sleepers consistently rated themselves as more alert than long sleepers did [4].

A beneficial effect of sleep on memory has been demonstrated, wherein specific sleep stages are differentially implicated depending on the memory system addressed by the task [26; 72; 20; 22; 71; 62; 47]. Many different memory models have been proposed and supported. One model makes the distinction between a declarative system, responsible for learning new facts and personal events, and a nondeclarative system, which includes procedural memories that are responsible for motor skills and habit learning [15]. A complementary memory model proposes that declarative memory is further separated into two different interacting systems: a semantic memory system (encompassing recall of concepts and general

knowledge) and an episodic memory system (linked to recall of specific events encoded in relationship to their temporal-spatial context) [67; 66]. Early sleep and memory studies showed evidence that deep NonREM sleep [10; 23] in the early part of the nighttime sleep cycle [78; 47; 48] improved performance of tasks typical of declarative memory, such as recall and recognition, whereas late REM sleep was found to be more supportive in tasks representing procedural knowledge [56; 57; 63]. Further support for the idea that NonREM sleep may have a beneficial effect on declarative memory comes from a study in which intermittent transcranial stimulation was applied during early NonREM sleep, and enhanced retention in a paired association task was reported [39]. Based on the above findings, this would suggest a dual model or parallel processing whereby each sleep stage acts independently to consolidate different kinds of memory. This is in contrast with a recent study showing that interfering with slow waves prevents sleep dependent improvements on a procedural memory task [6]. Nor does this theory explain earlier work showing performance improvements on a visual procedural memory task correlating with the amount of early NonREM sleep in the first quarter of the night and the amount of REM sleep in the last quarter of the nighttime sleep cycle (Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000). The relationship between individual sleep stages and memory consolidation is probably not that simple. It may be that the effects of sleep on memory depend on the temporal sequence of NREM sleep and REM sleep stages. Support for this idea comes from studies that provide evidence for the double step model (Stickgold, Whidbee, Schirmer, Patel & Hobson, 2000; Gais & Born, 2004) where optimal consolidation would require first SWS then REM sleep (Giuditta et al, 1995; Stickgold, 1998). In line with these findings is evidence for REM “windows” in animal studies, where REM sleep periods at specific times after training are important times for consolidation of memory to occur. REM outside of these windows is not necessary for memory consolidation (for review see Smith, 1996).

Many of the above of sleep studies require responses during a task and that the participant be skilled in motor or verbal domains. A typical behavioral reaction-time experiment consists of a stimulus followed by a response, without being able to observe the processing that occurs between them. Cognitive event-related potentials (ERPs) reflect neurophysiological activity elicited by the stimulus independent of behavioral response requirements. Additional knowledge may be gained from merging information about the behavioral performance and non-invasive electrocortical activity such as ERPs that will allow for the characterization of memory processes after sleep. ERPs provide a millisecond-by-millisecond reflection of the neural activity related to information processing stages. There is also reliable evidence that each component reflects the contribution of identified discrete cognitive processes (functional significance).

Event potentials have been recorded in a variety of memory tasks during wake [52; 51] and following longer periods of nocturnal sleep [43], and the results consistently show that differential responses to old (studied) and new items may be useful for studying memory and retrieval processes. The classical finding is an amplitude difference between ERPs elicited by stimuli on their first presentation (i.e., learning) and ERPs elicited on the second presentation of the same item (i.e., recognition) [24]. This modulation, usually referred to as the ‘ERP Old/New effect’, is typically observed whether the items to be recognized are pictures, faces, or verbal material [9; 25; 60]. This effect appears to have a specific role in

memory, since it has not been observed for incorrect judgements, i.e. misses and false alarms [76]. The ERP Old/New effect develops approximately 250 ms post-stimulus and lasts for approximately 800ms. It is composed of a series of ERP components or ‘effects’ distinct in their timing, scalp topography, task correlates, and dependence on pretraining instructions [16; 36; 55].

The classic ERP Old/New effect is produced by the modulation of two posterior components. The first is a central, parietal distributed negative wave (N400) elicited within 300–500ms that has been attributed to integration of the stimulus with the information already present in memory (semantic knowledge). A reduction in its amplitude for repeated (old) items could be interpreted as reflecting less integration effort necessary, due to its prior activation [8; 44] at encoding [54]. The second component involves a late positive component (LPC) also termed P600, elicited within 500–800 ms or longer [70]. The LPC/P600 has been attributed to an elaboration process of mnemonic binding that leads to formation or retrieval of an episodic trace consisting of the item and its context. More specifically, the LPC reflects a process of “memory synthesis” allowing regrouping of the various aspects of the information, which were extracted from previous processes to form a coherent memory representation of the event in long-term memory [54]. Furthermore, intracranial ERPs [30] have shown that the neural generator of the LPC/P600 involves, at least partly, the medial temporal cortex [14; 61], a brain region known to be involved with declarative memory. As established previously, the LPC/P600 amplitude is larger for old stimuli than for new stimuli [51; 35].

We previously demonstrated the sleep dependency of our task with a wake control group, and showed the beneficial effect of sleep over wakefulness on recognition memory performance [41; 40; 42]. The aim of the present study was to use behavioral performance data and ERPs following one night of sleep to examine the impact of individual differences in sleep duration on declarative (semantic, episodic) memory processes. Based on published evidence that enhancement in performance on tasks of declarative memory is associated with early NonREM sleep [47; 57; 48] and that short sleepers show a more rapid accumulation of NonREM SWS at the beginning of the night [3], we hypothesized that short sleepers would show even greater facilitation in performance for the studied items than longer sleepers. Furthermore, it is expected based on our previous work [40] that following a delay of sleep, the studied stimuli compared to the new will show an enhanced “Old/New effect” (i.e. the amplitude difference between previously learned old and new items).

2. Methods

2.1. Participants

Twenty-four subjects (12 males, 12 females), composed of habitually short (< 7 hours/night, $n = 8$), average (>7 but < 9 hrs/night, $n = 9$), and long (> 9 hr/night, $n = 7$) sleepers ranging in age between 18 and 39 years were tested in a recognition task after a delay of nocturnal sleep. All of the participants had completed some years of university education (mean education level: 18.3 $\pm$ 3.9 years). Participants were asked to keep regular sleep-wake schedules for at least a three-day period before coming to the laboratory. Following screening and prior to beginning the experiment, participants were required to complete

questionnaires intended to collect general sociodemographic information, sleep history, and possible problems with sleep (Sleep Questionnaire; Morning Questionnaire, Medical History). Participants were also required to fill out a sleep log prior to and during the course of the experiment. Sleep length was based on a sleep questionnaire and a 7- to 10-day sleep log. Sleep duration estimates included both weekday and weekend sleep. Eligible participants underwent an interview in the laboratory approximately ½ hour in duration. Exclusion criteria were a past or current history of psychiatric, neurological, or sleep disorder or other medical condition. Participants were also excluded if any of their first-degree relatives had a history of primary sleep disorder or major psychiatric illness. All had normal or corrected-to-normal vision. All participants were fully informed of the recording methods and signed a consent form before participating.

2.2 Procedure

To study effects on memory, we designed an experimental protocol focused on the effects of sleep on recognition memory without recording sleep stages in an attempt to minimize the potential negative “first night effects” of the recording apparatus on the quality of the subject’s sleep. The general protocol was built as a classical study-test design (Figure 1). ERPs were recorded in the test session only. The study (learning) phase and the test (recognition) phase, each lasting about 15 minutes, were separated by a delay of a night’s sleep in the laboratory. Information regarding the night of sleep in the laboratory was obtained by questionnaire on the subsequent morning (Table 1).

2.3. Memory Task: Study-Recognition Test

Subjects sat in a comfortable chair in a sound-attenuated room. Stimuli were presented on a gray background at the center of this screen 56 cm away from the subjects, sustaining a visual angle of 5° and an interval inter-stimulus of 4–5 sec. Each stimulus remained for 1000 ms and was replaced by a mask with the word ‘blink’ for 600ms. During the study (learning) phase, the subjects were asked to memorize each stimulus for a subsequent recognition test while indicating whether each face was that of a man or a woman by pressing arrow keys on the computer keyboard. This task ensured that the subjects attended to each stimulus presented during the study phase. Following a night of sleep, the subjects underwent a recognition test session. The participants were required to indicate as accurately and quickly as possible whether each stimulus had been previously presented (‘old’) or not (‘new’) by pressing arrow keys on the computer keyboard.

2.4. Stimuli

We used unfamiliar face stimuli, which offer the advantage of permitting extraction of semantic information such as, age, gender, expression, or resemblance to known persons [12], while their unfamiliarity necessitates the formation of a new trace that fosters episodic processes. ERPs provide information (indices) related to the two aspects of declarative memory processing (i.e. semantic/episodic) [28; 29].

The stimuli were taken from a bank of color photographs of faces, which is composed of front views taken under the same conditions of background and light. Each face had been previously scored as neutral, friendly, or unfriendly in a prior study [17]. The 80 faces

chosen as stimuli in this experiment had relatively high neutral scores and were balanced for gender. The set was used to construct a study session series of 40 stimuli and a test session series of 80 stimuli in which the 40 previously presented were intermixed with an additional 40 'new' stimuli.

2.5. Recordings and signal extraction

The electrophysiological signals were recorded by means of an amplifier (S.A. Instrument Inc. San Diego, CA). The ERP was recorded from midline scalp electrodes (Fz, Cz, Pz) placed according to the 10–20 International System [7; 33]. All channels were referenced to the linked earlobes. Vertical and horizontal eye movements were monitored via electrodes placed below and on the outer canthus (respectively) of both eyes. During the recording, the impedance of all electrodes was maintained below 5 K Ω . The EEG was recorded continuously with a bandpass of 0.01–30 Hz, digitized on-line at a rate of 250 Hz and stored along with the codes identifying the experimental condition, the stimulus onset, and the subject's response for subsequent off-line averaging. Off-line averaging using statistical software algorithms (InstEP software) was performed after EOG correction (Woestenburg method) and after rejection for epoch with amplifier blocking exceeding 100 ms (71). ERPs for correctly rejected new items and correctly recognized old items were then computed separately from 0 to 1000 ms post-stimulus onset with a –200ms pre-stimulus baseline.

2.6. Statistical Analysis

All subjects filled out a sleep log reporting subjective estimates of the number of hours of sleep prior to testing and throughout their participation in the experiment, which included one night of sleep in the laboratory. The mean numbers of hours of sleep were analyzed with two-tailed paired t-tests to determine whether there were any statistically related differences between sleep in the laboratory and at home. Paired t-tests for dependent measures were used to analyze the subjective sleep data (i.e. the number of nocturnal awakenings, sleep onset latency) in the laboratory compared to a normal night of sleep at home.

The behavioral performance data were obtained simultaneously with ERP data. Accuracy included the percent hits (i.e. correctly recognized old items), percent false alarms (i.e. the new items incorrectly identified as old), and percent missed (i.e. not recognized response to old items) and were compared by means of an ANOVA in all three groups following sleep. This enabled us to determine whether sleep duration influenced the memorization of items among the three groups. Reaction time (RTs) means were obtained in the three groups after a night of sleep for old (studied) and new stimuli and were compared by method of a factorial design with 2 'stimuli' (Old, New) and 3 'groups' (short, average, long) mixed ANOVA. The RT responses were collected for correct trials only.

ERP peaks were identified by visual inspection of each participant's waveforms recorded at Cz within the interval from stimulus onset to 1000ms. This latency window was selected as typical in previous studies of ERP Old/New effect following a long delay of sleep [43]. The N400 and LPC/P600 amplitudes were quantified with respect to the baseline within time windows of 300–400ms and 400–800 ms, respectively.

The ERP amplitudes were analyzed by a 3 group (short, average, long) x 2 stimuli (Old, New) x 3 site (Fz, Cz, Pz) mixed ANOVA with repeated measures (stimuli). The Greenhouse non-sphericity correction was employed in repeated measures ANOVA when appropriate [27]. Following convention, unadjusted degrees of freedom are reported along with the Greenhouse-Geisser adjusted p-value. In the case of significant interactions, post-hoc analysis was conducted where appropriate. Statistical significance was set at alpha 0.05.

3. RESULTS

3.1. Experimental Measures

Results of a paired t-test of the short sleepers concluded that there was no significant difference between mean number of hours of sleep on the sleep log and those reported in the morning after sleeping in the laboratory [$M = 6.8$, $SD = 0.23$ vs. $M = 6.9$, $SD = 1.2$; $t(7,8) = -0.43$, $p = 0.67$, n.s.]. A paired t-test revealed significant differences in the mean number of hours of sleep reported on the sleep log and those in the laboratory among both the long and average sleepers [$t(6,7) = 4.6$, $p < 0.01$; $t(8,9) = 3.2$, $p = 0.01$, respectively]. As for the time it takes to fall asleep in the laboratory, results of independent t-tests revealed a difference in sleep onset between short and long sleepers, [$t(7,6) = 5.88$, $p = 0.01$] and a trend when comparing the short and average sleepers' sleep onset, [$t(7,8) = 2.78$, $p = 0.09$]. On the other hand, an independent t-test showed no significant difference in sleep onset between the average and long sleepers [$t(8,6) = 0.41$, $p = 0.95$, n.s. (Table 1)]. There were no significant differences in the time it takes to fall asleep in the home compared to night of sleep in the laboratory in any of the groups (paired t-tests, p 's > 0.52 , n.s.). The long sleepers reported their sleep to be similar or better in the laboratory (Table 1). In contrast, the average sleepers reported their quality of sleep in the laboratory to be similar or, worse than that at home.

The paired t-test to evaluate possible differences between the subjects' estimate of awakenings (number of times) during the night of sleep in the laboratory and sleep at home from the sleep log (see Table 1) showed no significant difference among long [$t(6,7) = -.47$, $p = 0.64$] or short [$t(7,8) = .26$, $p = 0.80$] sleepers. In the average sleepers, however, the paired t-test revealed a significant difference in the number of nocturnal awakenings between the laboratory ($M = 2.3$, $SD = 1.1$) and home [$M = 1.1$, $SD = 1.1$, $t(8,9) = -3.3$, $p = 0.01$].

3.2. Behavioral Data

ANOVA on scores (% correct) revealed a significant within-subject factor of stimuli (Old/New) [$F(1,21) = 15.18$; $p < 0.01$] and a significant between group factor (short, average, long) [$F(2,21) = 5.6$; $p = 0.01$]. Follow-up post hoc (Tukey HSD) tests revealed significant differences between the short sleepers and average sleepers ($M = 79.5$, $SD = 12.7\%$ vs. $M = 66.8$, $SD = 8.5\%$, $p < 0.02$) and between the short and long sleepers ($M = 79.5$, $SD = 12.7$ vs. $M = 61.4$, $SD = 14.5\%$, $p < 0.03$) on studied items (Figure 2). No significant difference was found when comparing the average vs. long sleepers on accuracy of performance. Follow-up analysis on the studied items revealed that the long sleepers failed to show significant retention of the old memories, with their recognition of old faces not different

from chance (t-test, $p = 0.12$; binomial test, $p = 0.23$), while the short sleepers showed highly significant performance (t-test, $p < 0.01$, binomial test, $p < 0.01$).

ANOVA performed on the Old/New scores (%correct) by age revealed no significant difference in accuracy on the old stimuli [$F(9, 23) = 2.87$; or the new stimuli [$F(9, 23) = 1.11$; p 's > 0.06] by age. ANCOVA performed on the accuracy of the Old/New scores (%correct) by group with age as a covariate revealed a trend in accuracy performance [$F(2, 20) = 0.44$; $p = 0.06$.] and no significant interactions involving the other factors (p 's > 0.70), indicating that the Old/New effect was seen across all groups.

The relationship between accuracy of the scores (% correct) and sleep duration (sleep log hrs) in the short, average and long sleepers was investigated using Pearson product-moment correlation coefficients. There was a moderate but significant negative correlation between the old stimuli and the hrs of sleep on the sleep log ($r = -0.45$, $p < 0.03$), with increased accuracy associated with decreased sleep duration (Figure 3).

A closer look at the individual groups revealed a negative correlation between the old/new stimuli and short sleep duration ($r = -0.66$, $p < 0.04$). In contrast, the longer sleepers showed a positive correlation between the two variables (Average sleepers, $r = 0.65$, Long sleepers, $r = 0.79$, p 's > 0.03), indicating increased accuracy associated with increased number of hours of sleep (not shown).

After removing two long sleepers with accuracy lower than 50%, ANOVAs on correctly answered RT data showed a significant effect of stimuli (Old/New) [$F(1, 19) = 4.45$; $p < 0.05$, $n = 22$]. There was no significant interaction involving the group factor, indicating that the facilitatory response to the previously studied stimuli compared to the new items was present in all three groups. Figure 4 shows faster RT responses to the old compared to the new stimuli after a night of sleep among all sleepers.

3.3. ERP Data

The grand average waveforms for the correct responses presented in Figure 5 show the classic Old/New memory effect (i.e. a positive shift from 250 to 800ms) similar to those previously reported after a night of normal sleep [42; 40]. ERP peaks were identified by visual inspection of the individual traces recorded at Cz within the window from stimulus onset to 1000 ms. This epoch was selected as typical from our previous studies of ERP Old/New effects. The N400 and LPC/P600 amplitudes were quantified with respect to the baseline within their respective time-windows. The N400 peak is seen as a negative deflection, peaking at ~400–500ms post-stimulus followed by a LPC or P600 (~500–800ms). To obtain neural activity related to the Old/New effect we subtracted the ERPs amplitudes in response to the old stimuli from the ERP's responding to the new stimuli for each component and plotted it as the Old/New Difference (Figure 6).

ANOVA on the Old/New effect obtained in the N400 time window showed significant effects of site [$F(2, 42) = 6.92$; $p < 0.01$] and stimuli (Old/New) [$F(1, 21) = 20.01$; $p < 0.001$] (Figure 6). Post-hoc analysis performed on the three midline sites revealed that the Old/New effect was significant at the Fz, Cz and Pz regions [$F(1, 21) = 18.9$, $F(1, 21) =$

19.2, $F(1,21) = 5.7$; p 's < 0.03 , respectively]. Post-hoc analysis performed on the combined Fz-Cz sites and combined Cz-Pz sites revealed that the N400 effect was significant at the centro-posterior region (Cz-Pz) ($F(1,21) = 26.83$; $p < 0.001$), which is the usual distribution for the posterior N400 Old/New effect. Although the N400 Old/New effect appears generally larger at the fronto-central sites (Fig 6, left), there were no interactions involving group by stimuli (Old/New) [$F(2, 21) = 0.83$; $p = 0.44$, n.s.] or group by site [$F(4,42) = 0.69$; $p = 0.56$, n.s.].

ANOVA on data obtained in the P600 time window showed significant effects of site [$F(2, 42) = 6.36$; $p < 0.01$] and stimuli (Old/New) [$F(1, 21) = 8.31$; $p < 0.01$]. Follow-up analysis revealed that the site effect was significant at the Fz and Cz sites, [$F(1,21) = 9.9$; $p < 0.01$, $F(1,21) = 6.0$; $p = 0.02$] and only a trend at Pz site ($F(1,21) = 3.9$; $p < 0.06$). Once again, there was no significant interaction involving the group factor, indicating that the P600 Old/New effect is similar across all sleepers (Figure 7).

4. Discussion

The present study investigates the effects of individual differences in habitual short, average, and long sleepers on recognition memory (with the aid of ERPs) using unfamiliar faces. The goal of the study was to use behavioral performance data and ERPs to examine the impact of individual differences in sleep duration on semantic and episodic (declarative) memory processing.

The quality of sleep in the present investigation was defined subjectively. Our results show that short sleepers reported falling asleep more quickly in the laboratory (~10 minutes) than the long and average sleepers (~30 minutes). This is consistent with other studies showing shorter sleep latencies in short sleepers compared to long sleepers [1; 3]. The long sleepers here reported similar or better quality of sleep in the laboratory than in the home. Some of the subjects in both the average and short groups reported lower-quality of sleep in the laboratory. In the average sleepers the poorer quality of sleep may be due to the significant difference in the number of nocturnal awakenings that occurred in the laboratory.

The short sleepers had fewer missed (forgotten) responses on the studied items compared to the long sleepers, performing better than the longer sleepers on this recognition task of declarative memory. Research has shown that performance on recognition and recall memory tasks and slow wave sleep decrease with age. Because the mean age of the participants in the 'Short' group was older than the other two groups, we would expect short sleepers to be worse at this task.

Plihal and Born (1997) studied the effect of early night sleep and late night sleep on two cognitive tests: the recall of a list of associated word pairs (declarative memory) and mirror-tracing skills (procedural memory) [47]. They showed that early sleep was associated with better performance on the declarative memory test than late sleep, while late sleep was associated with better performance in the procedural memory test. These results suggest that sleep in the early and later parts of the sleep cycle, and/or specific sleep stages since slow-wave sleep (SWS) is more prevalent in early sleep and REM sleep is more prevalent in late sleep, may have a specific effect on memory systems. Along the same lines, the greater

enhancement of performance seen in short sleepers in the present study may be due to their more rapid accumulation of NonREM slow wave sleep at the beginning of the night [4]. Tononi *et al.* have proposed that slow waves reduce overall synaptic strength to a baseline level thereby preventing development of over potentiated neural networks and leading to an increase in signal-to-noise ratios that could result in next-day performance improvement [65]. Some authors propose that memory consolidation might depend on the orderly succession and alternation of NonREM and REM sleep stages though the night [XX; XX]. (Stickgold et al., 2000, Gais et al., 2000). Accordingly, SWS would be first stage of data processing. During NonREM SWS it is suggested that there is elimination of useless or superfluous memory traces and a strengthening of those traces that are relevant (a process of discrimination). During the second step, REM sleep consolidates the memory trace in the neuronal network (consolidation process). *Why do the short sleepers perform better when research has shown that short and long sleepers get the same amount of SWS?* It may be that the rapid elimination of the irrelevant information in the first part of the sleep cycle results in a more efficient discrimination process in the first step thereby leading to increase signal strength (a better quality signal) for next step, the consolidation process.

One could argue that the better performance in the short sleepers resulted from their sleep in the laboratory being more restful than for the other two groups. A higher homeostatic response can in fact be induced experimentally in average sleepers by curtailment of their sleep [13; 18; 69]. But while the laboratory sleep was reported to be of poor quality in a similar numbers of subjects in the average and the short groups, the short sleepers were more accurate in their performance on the test. Similarly, when comparing the short and long sleepers, ¼ of the short sleepers reported their sleep to less restful or of lesser quality (Table 1) than normal, while none of the long sleepers did so, yet the short sleepers performed better on the memory task the next morning.

Based on our correlative data, we show support for two groups, whose performance differs on this declarative memory task. In our short sleepers, performance increased with decreasing sleep. In contrast, our average and long sleepers showed increased improvement as the number of hours of sleep increased. One explanation for the differences in short and long sleep durations relates to timing of the circadian rhythms [5]. It has been reported that the circadian pacemaker programs a longer biological night in the long sleepers [5]. Circadian rhythms arise from transcriptional and translational feedback cycles of clock genes in cells of the suprachiasmatic nucleus, which programs daily day/night cycles [50]. Recently, polymorphisms in human clock genes have been associated with different circadian phenotypes, i.e. short and long sleep durations. A mutation in the *hPer2* gene is seen in individuals with familial advanced sleep phase syndrome that appears to shorten the circadian period [64]. Other clock genes have been associated with a prolonged circadian period [37]. Thus, these genes may result in differences in circadian rhythms and inter-individual differences sleep duration.

As expected from the literature, RTs differed significantly between old and new faces. However, there was no evidence for a beneficial effect across the three groups on RTs [24]. Some have argued that accuracy scores relate to the accessibility of the information or qualitative aspects of the memory trace [68], while RT reflects the quantity or complexity of

the processes necessary to access information in memory [38]. This would account for our data showing a lack of RT differences across the three groups, but a significant Old/New effect. Further, it would argue for a qualitative difference in accuracy in the short sleepers rather than the quantity of information retrieved. In fact, the RTs in the short sleepers were slower than in the other groups, though the difference did not reach significance (see Figure 4). It may be that the short sleepers are more careful in their decision-making process. Evidence for this idea comes from that fact that 29% of the subjects in the long sleeper group had fewer than 50% correct responses, and that 4 of the 5 poorest performers were long sleepers. Strikingly, the long sleepers, as a group, failed to show significant retention of the studied stimuli, with their recognition of old faces not different from chance, while the short sleepers showed highly significant performance.

Our results showed that the ERPs to old stimuli differ from the ERP to new stimuli in the same way numerous other researchers have shown this Old/New effect using shorter delays [9; 25; 35; 51; 53; 59] and longer delays [43; 40]. However, it appears that the Old/New ERP memory effect in habitual short, average and long sleep duration influence declarative memory processes in a similar manner.

As mentioned in the introduction, the two major ERP components representing the classic Old/New effect that have been consistently reported in the literature are the posterior N400 and the LPC/P600 [24]. The results show an Old/New effect involving the posterior N400 component similar to the effect classically observed [54]. The amplitude of the N400 component was decreased to previously presented stimuli (i.e., old stimuli) corresponding to the fact that the studied items were more easily integrated with semantic knowledge than the new stimuli [19; 32; 54]. Nevertheless, there were no significant group differences in the N400 Old/New effect, which suggests that there is no facilitation by habitual differences in sleep duration on the semantic integration process. The N400 Old/New effect (Figure 6, left) in the average sleeper appears less than that of the short and long sleepers at the Cz and Pz sites. However, the N400 amplitude was not found to significantly different from the other two groups. Our sample size, although adequate in relation to other Old/New ERP memory studies, may explain the failure to find a significant difference on the ERPs across group.

The N400 is typically followed by a late positive component, LPC or P600, that exemplifies the Old/New modulation generally observed in memory studies [46; 49]. The functional interpretation of the P600 is that its amplitude is proportional to the elaboration of the information retrieved from episodic memory [54]. By this account, the larger P600 amplitude to old stimuli compared to new stimuli simply reflects that previously memorized information was more elaborated than the new ones during retrieval in all sleepers.

4.1. Conclusions

Although all groups showed faster responses and larger Old/New effect to studied stimuli compared to new items, the short sleepers identified previously studied stimuli more accurately than the other two groups. Our data show for the first time that individual differences in recognition memory performance may be associated with differences in individual sleep duration. These findings may have important implications, because they

suggest that it may not be the amount of sleep that is important but rather individual differences in sleep regulation or tolerance for sleep pressure.

Limitations—Our experiment looked at the effects of individual differences in sleep duration on memory using subjective reports and behavioural performance data in an attempt to minimize the potential negative effects of the sleep recording apparatus on the quality of the subject's sleep. However, several sleep variables such as sleep stages, spindles, number of rapid eye movements, and slow wave activity have been shown to be important in learning and memory processing. Furthermore, circadian effects and effects of sleep could not be completely separated in the present study, which limits the conclusions that can be drawn from the present data. Future studies should examine if this effect is related to sleep structure and/or sleep regulation.

Acknowledgments

This research was supported by the Fonds de Recherche en Santé du Québec, FRSQ and NIH grant R-01-MH48832. The authors' thank Dr. Daniel Aeschbach for his helpful comments and Dr. Roger Godbout for his much-appreciated support and guidance. We also wish to thank Paul Guttry and his staff for reviewing the manuscript.

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Fig. 1.
Experimental protocol for the study test task.

Fig. 2.

Behavioral performance (mean % and SEM) results showing more accurate responses to the studied “old” faces among Short Sleepers compared to the Average Sleepers or Long Sleepers following a period of normal sleep. Follow-up post-hoc Tukey’s HSD tests were used to evaluate the group differences: Short vs. Long Sleepers, * $p < 0.03$; Short vs. Average Sleepers, + $p < 0.02$. Short Sleepers ($n = 8$), Average Sleepers ($n = 9$), and Long Sleepers ($n = 7$).

Fig. 3. Reaction time performance (mean % and SD) results showing faster responses to old or previously studied stimuli following a period of nighttime sleep.

Fig. 4. Pearson Product Moment bivariate correlation between the accuracy (% correct) of the studied stimuli and the sleep from sleep log. Short Sleepers - black circles; Average Sleepers - grey circles; Long Sleepers - empty circles. $N = 24$

Fig. 5.

Grand Average ERPs elicited by correctly recognized 'old' stimuli (black line) & 'new' stimuli (gray line) at the posterior EEG sites (Cz, Pz) across the three groups; Short Sleepers ($n = 8$), Average Sleepers ($n = 9$), and Long Sleepers ($n = 7$).

Old/New ERP Memory Effect

Fig. 6. ERP Old/New Difference in mean amplitude (old minus new) for the N400 (left) and LPC/P600 (right) components from midline sites (Fz, Cz, and Pz) following sleep in three groups: Short Sleepers (empty square), Average Sleepers (black triangles), and Long Sleepers (black square).

Table 1

Demographic & sleep data on short, average and long sleepers.

	SHORT n= 8	AVERAGE n= 9	LONG n= 7
AGE (Mean +/-SD)	30.3+/-5.8	23.1+/-4.0	21.7+/-2.1
GENDER (12 female ♀/12 male ♂)	3 ♀/5 ♂	5 ♀/4 ♂	4 ♀/3 ♂
SLEEP LOG (Mean+/-SD)	6.8+/-0.23	8.1+/-0.45	9.1+/-0.52
Weekends (hrs)	7.1+/-0.48	8.1+/-0.45	8.7+/-1.2
Weekdays (hrs)	6.4+/-0.46	7.9+/-0.46	9.3+/-0.72
SLEEP LABORATORY (Mean+/-SD)			
Hours of Sleep	6.9+/-1.2 n.s.	8.3+/-0.70***	8.9+/-0.39**
Sleep Onset (min)	10.5+/-6.8	32.2+/-34	31.4+/-18.4
SLEEP QUALITY (No. of Subject) (home vs. lab)			
Better than Usual	12% (1:8)	None	14% (1:7)
Similar in Quality	63% (5:8)	66% (6:9)	86% (6:7)
Lesser Quality	25% (2:8)	33% (3:9)	None
NUMBER OF AWAKENINGS			
Laboratory	1.5+/-1.2 n.s.	2.3+/-1.1 *	1.6+/-1.5 n.s.
Home	1.7+/-1.6	1.1+/-1.1	0.9+/-0.8

Mean ± SD is presented. Paired t-test between home Sleep Log & Sleep Laboratory:

*
p = 0.001,**
p = 0.003,***
p = 0.005