

Homeostatic and Circadian Influences on Dreaming: NREM Mentation During a Short Daytime Nap

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Summary. It has long been known that dream recall, along with various other features of dreaming, changes as a function of time of night. Yet the processes which might account for these time-dependent variations remain obscure. Here we assess the contribution of homeostatic and circadian factors to the generation of NREM mentation across the diurnal cycle. Assuming that previously reported time-of-night mentation effects are primarily driven by a circadian activation cycle which approximates the core body temperature (CBT) rhythm, it was hypothesized that more content would be reported from daytime nap awakenings as compared to night awakenings. Afternoon Nap reports were compared to previously-collected nocturnal reports from Circadian Nadir and Late Morning time points. Contrary to our hypotheses, both amount of mentation reported and propensity to report any mentation at all were lower in Nap as compared to Late Morning reports. A purely circadian influence following the CBT cycle is inadequate to explain this pattern of mentation production.

Keywords: Sleep; Dreaming; Sleep stages; REM; NREM; Circadian; Homeostatic; Mentation

1. Introduction

Previous empirical work on the neural basis of dreaming has focused largely on describing and explaining differences between mentation reported from REM, as opposed to NREM sleep (Braun et al., 1997; Dement & Kleitman, 1957; Hobson, Pace-Schott, & Stickgold, 2000). This approach has often been accompanied by the presumption that neural mechanisms specific to REM sleep are the primary generators of dreaming, an influential notion originating with the discovery that dreaming has a high probability of being reported from REM (Dement & Kleitman, 1957). Unfortunately, the large magnitude of the REM/NREM dreaming effect appears to have dissuaded investigators from identifying other neural bases for systematic variations in the production of sleep mentation. In particular, one modulator of dream production other than the REM/NREM cycle is evident in observations that dreaming increases dramatically across the night within NREM, as well as within REM sleep (Antrobus, Kondo, Reinsel, & Fein, 1995; Casagrande, Violani, Lucidi, Buttinelli, & Bertini, 1996; Pivik & Foulkes, 1968; Stickgold, Malia, Fosse, Propper, & Hobson, 2001; Wamsley, Hirota, Tucker, Smith, & Antrobus, 2007). The present study further examines the basis of changes in NREM dreaming across the diurnal cycle, in an effort to specify the nature of this modulatory influence on the dreaming process.

It has long been known that dream reports change on a number of dimensions as the night progresses (Antrobus et al., 1995; Casagrande et al., 1996; Pivik & Foulkes, 1968; Stickgold et al., 2001; Wamsley et al., 2007). Later in the night, propensity

for mentation recall, dream report length, and various qualitative features of dream reports increase, often dramatically. It has been proposed that such time-of-night mentation effects may be caused by an endogenously-driven, circadian activation rhythm (Antrobus et al., 1995; Nielsen, 2004). Indeed, increases in mentation production during the late morning hours are observed even when the influence of time since sleep onset is controlled for (Antrobus et al., 1995; Suzuki et al., 2004), suggesting that the time-of-night effect on dreaming is controlled by internal clock-like mechanisms.

If reported sleep mentation is modulated, at least in part, by an endogenous circadian rhythm, it is reasonable to postulate that the time course of this rhythm might approximate the core body temperature (CBT) cycle. A number of other cognitive functions, such as alertness, dexterity, and working memory performance follow an endogenously-driven time course correlated with CBT (Monk et al., 1997; Wright, Hull, & Czeisler, 2002). Furthermore, some features of the sleep EEG itself also vary according to a circadian rhythm, reaching maximum levels in the late morning, coincident with the rising arm of the CBT rhythm (Czeisler & Khalsa, 2000; De Gennaro & Ferrara, 2003; Deboer, 2002; Dijk, Shanahan, Duffy, Ronda, & Czeisler, 1997).

However, because studies of dreaming across the night rarely control for the influence of time since sleep onset, most evidence for 'time-of-night' effects on dreaming could also be explained via homeostatic-driven changes in arousal, changing in concert not with circadian time, but rather with time since sleep onset. That is, in studies of dreaming across the night, circadian and homeostatic influences on the dependent variables have typically been confounded, prohibiting meaningful conclusions regarding the cause of changes in dreaming across the night. In fact, there are good reasons to think that homeostatic changes in sleep need across the night might contribute to time-of-night mentation effects. Propensity for slow wave activity (SWA) has generally been taken to be the physiological marker of homeostatic sleep need, building up following an exponentially saturating function during wakefulness, and discharging during subsequent sleep (Benington, 2004; Borbely, Baumann, Brandeis, Strauch, & Lehmann, 1981). Dis-

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tance from periods of REM sleep and, by implication, proximity to slow wave sleep, has been cited as a strong predictor of decreased dream recall within NREM (Nielsen, 2000). Though the mechanisms underlying a potential influence of slow wave propensity on dream recall outside of stages 3 and 4 remain unknown, some studies examining dream recall across the night are broadly more consistent with a homeostatic-based rather than a circadian-based explanation for time-of-night effects on dreaming. Pivik & Foulkes (Pivik & Foulkes, 1968) and Nielsen et al. (Nielsen, Germain, & Zadra, 1997) have both reported a sharp increase in dreaming early in the night, remaining relatively stable thereafter, a pattern which roughly mirrors the initial steep decline in SWA seen in the early night (Nielsen, 2004).

In a recent study, we reported that the amount of information recalled from NREM sleep increases dramatically in the late morning relative to the middle of the night near the circadian nadir of the CBT rhythm. This time-of-night effect on amount of information reported upon awakening was very large ($\eta_p^2 = .51$), larger even than the effect of sleep stage on dream recall ($\eta_p^2 = .40$) (Wamsley et al., 2007). However, in this study, the influence of time since sleep onset was not controlled for, and so the large time-of-night effect may have been in part due to the discharge of homeostatic sleep need across the night. Previous studies which controlled for the influence of time since sleep onset through the use of full or partial forced desynchrony protocols have found relatively smaller effect sizes for circadian influences on dreaming (Antrobus et al., 1995; Suzuki et al., 2004).

In order to assess the relative contributions of circadian and homeostatic processes to diurnal variations in sleep mentation, here we examine dream reporting during a period of high circadian activation preceded by several hours of wakefulness, rather than after a full night of sleep. We compared the characteristics of mentation recalled from short daytime naps containing exclusively NREM sleep to nighttime NREM mentation previously collected from both the Circadian Nadir of the core

body temperature (CBT) rhythm and the Late Morning, under an identical protocol (Wamsley et al., 2007). We reasoned that, if sleep mentation is indeed driven by a circadian cycle approximating the time course of the CBT rhythm, mentation production should be greater during an early afternoon nap than in the late morning hours. Alternatively, to the extent that dreaming is driven by factors related to the homeostatic discharge of SWA across the sleep period, mentation production during NREM naps would be expected to be lower than in the late morning following a night's sleep, due to buildup of sleep propensity occurring during the hours of wakefulness preceding a nap period.

2. Methods

2.1. Participants

20 healthy undergraduate students (mean age: 27.6 ± 9.6 years), kept a detailed sleep log during the week prior to the study. In order to qualify for participation, subjects were required to demonstrate an average bedtime before midnight, with no bedtime during the week deviating from that average by more than one hour. Participants were asked not to consume any caffeine on the morning of the study, or alcohol on the night prior to the study.

Data from these participants were compared to overnight mentation data previously collected from a similar group of participants ($n = 20$) (Wamsley et al., 2007). Table 1 describes the characteristics of Overnight vs. Nap participants. These two subject groups were not significantly different on age, gender, sleep schedule, or dream recall variables. Selection criteria for the two groups were identical. Both studies were approved by the institutional review board of the City College of New York.

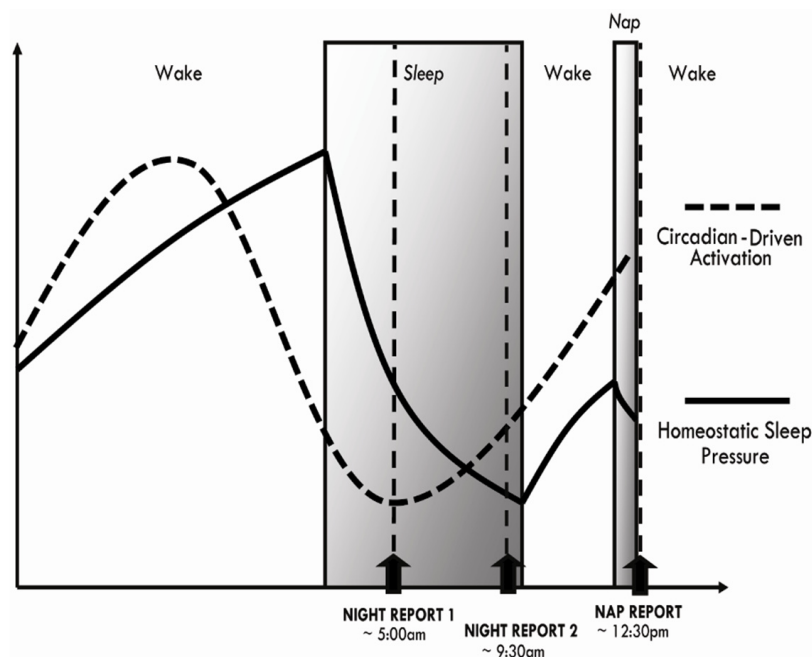


Figure 1. Report collection periods in relation to the presumed time courses for both circadian-driven activation and homeostatic sleep need.

Table 1. Characteristics of Nap vs. Overnight Subjects.

	Nap Subjects (n=20)	Overnight Subjects (n=20)
Mean Age	27.6 ± 9.6	26.7 ± 7.5
Mean Wake Time (hours)	7:48 ± 0.27	7:10 ± 0.22
Mean Bedtime (hours)	11:48 ± 0.16	11:38 ± 0.15
Dream Recall	2.5 ± 1.5	3.2 ± 1.6
Waking Verbal Generation (WVG)	21.39 ± 3.50	27.38 ± 5.94
% Female	75%	75%

Note. Means (\pm SE) characteristics of Nap vs. Overnight subjects. Dream recall values represent the mean number of nights which subjects reported recalling a dream during the week prior to the study. There were no significant differences between groups on any variable ($p > .2$ for all comparisons).

2.2. Procedures

Participants arrived at the laboratory at 11:00am, where they were familiarized with the lab and signed consent. Polysomnographic variables were measured using a standard EEG (C3-A2, C4-A1), EOG, and EMG montage. Signals were amplified using Grass Model 7 amplifiers and digitally converted for acquisition and analysis using Grass-Telefactor's *Gamma* software.

Data collection began at approximately 11:30am, as subjects reclined in a darkened, sound-attenuated sleep chamber. Just prior to the nap opportunity, subjects gave three reports on their waking mentation experiences after 3, 5, and 10 minutes of lying quietly awake in the darkened sleep chamber. The three-minute report was always given first as a "practice" session, and order of the subsequent 5 and 10 minute waking reports was counterbalanced across subjects. The nap opportunity then began at approximately 12:00pm. All experimental awakenings from sleep were made from stage 2, following at least 20 minutes of continuous NREM. If participants were unable to initiate sleep within 45 minutes, to maintain sleep for a sufficient duration, or entered either SWS or REM less than 20 minutes following sleep onset, the study was terminated. Identical sleep stage criteria had previously been used to obtain NREM reports from Overnight subjects (Wamsley et al., 2007). Figure 1 illustrates the three NREM report collection periods relative to presumed time courses for homeostatic and circadian influences on cortical activation. Nap reports were collected from a period of high circadian activation and also higher SWA propensity, relative to Late Morning reports collected after a full night of sleep.

Procedures for collecting waking and sleeping mentation reports were identical. In each case, subjects were contacted by calling their name over a microphone once per second until they responded. Upon awakening, subjects responded to the pre-recorded question "Please tell me everything that was going through your mind just before I called."

Subsequently, subjects filled out a written form assessing the visual and emotional qualities of their mentation. To assess the visual qualities of their experience, participants were asked to list up to three of the most salient objects or persons in the mentation, and to indicate whether these were visual images. If any images were visual, participants rated the perceptual quality of these images by picking out the picture that most resembled their visual experience from a 4x4 array of photographs varying in brightness and clarity. Photographs were scaled such that photo selections could then be converted into separate scores for "Brightness" and "Clarity", for which a score of 100 represents brightness and clarity typical of waking visual experience (Antrobus et al., 1995). Participants then rated the presence and intensity of nine emotions using a nine-point Likert scale (Smith et al., 2004). Total Emotional Intensity was calculated by adding participants' ratings of the

intensity of the nine separate emotions. Emotion scores were log-transformed to remove a positive skew.

2.3. Scoring of Mentation Reports

Verbal mentation reports were transcribed and scored for Word Information Count (WIC), Waking Verbal Generation (WVG), Dreamlike Quality, and Bizarreness. Two independent raters, blind to condition, were trained on each measurement scale prior to scoring the data. Reports without mentation content were scored zero on all scales.

Word Information Count (WIC). WIC is a modified word count measure that eliminates repetition, non-words, and words that do not provide new information about the sleep mentation. WIC is a revised version of Total Recall Count (TRC), demonstrated by Antrobus (Antrobus, 1983) to be one of the best discriminators of REM and NREM reports. WIC scores were log-transformed ($\log WIC = \ln(x+1)$) to remove a positive skew. Inter-rater reliability for WIC was .95.

Waking Verbal Generation (WVG). WVG was calculated by taking the mean log-transformed WIC score of the 5 min and 10 min pre-sleep waking reports. This variable was created in order to measure subjects' general propensity for reporting mental experiences, independent of their dream recall per se.

Dreamlike Quality. Dreamlike Quality is a global measure for which judges are instructed to rate reports on a scale of 1-10, according to how "dreamlike" the report seems (Reinsel, Wollman, & Antrobus, 1992). Inter-rater reliability for Dreamlike Quality was .80.

Bizarreness. Bizarreness is a count of bizarre elements of three types in the mentation: discontinuities, improbable combinations of elements, and indefinite identities of characters (Reinsel et al., 1992). Bizarreness scores were log-transformed to remove a positive skew. Inter-rater reliability for Bizarreness was .71.

3. Results

3.1. Characteristics of Nap vs. Overnight Subjects

Nap and Overnight subjects were similar on age, gender distribution, habitual bedtime, habitual waking time, and trait dream recall as assessed by the sleep log (Table 1). Although Nap and Overnight subjects also did not differ significantly on WVG (Table 1), the amount of content which subjects reported from wakefulness was strongly predictive of the amount of sleep mentation they subsequently reported (as measured by WIC) and was significantly or near-significantly correlated with each of the qualitative measures considered here, with the exception of Clarity (WIC: $r = .33$, $p = .04$; Dreamlike Quality: $r = .30$,

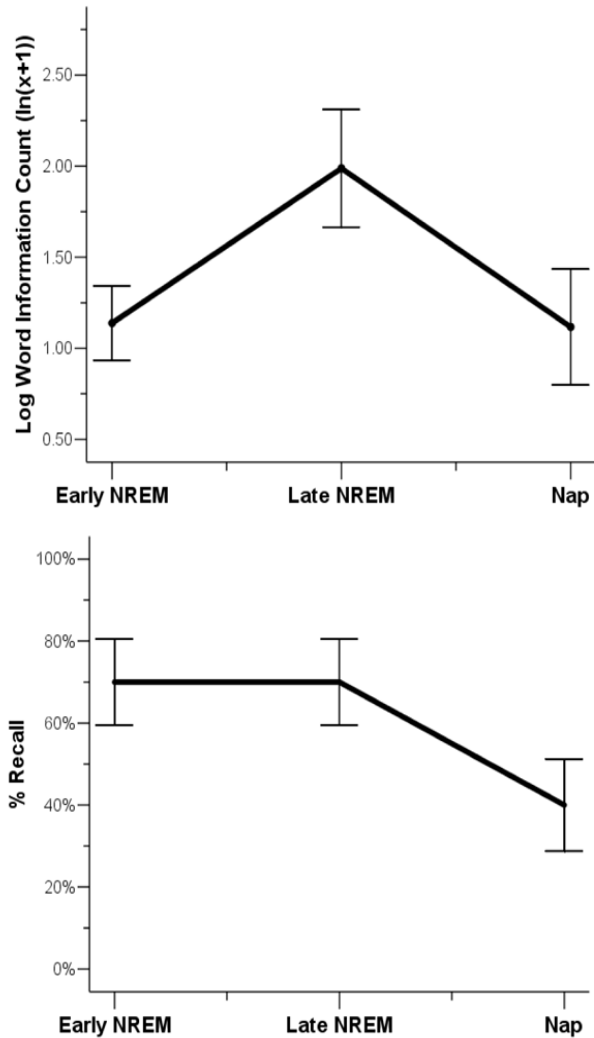


Figure 2. Top: Mean Word Information Count (\pm SE) from each report collection period. Bottom: % Dream Recall (\pm SE) from each report collection period.

$p = .06$; Bizarreness: $r = .33, p = .04$; Emotional Intensity: $r = .33, p = .04$; Brightness $r = .29, p = .07$; Clarity: $r = .07, n.s.$). Accordingly, in order to eliminate the influence of individual differences in WVG, NREM nap reports were compared with Nadir and Late Morning overnight reports using a between-subjects ANCOVA model controlling for WVG as a covariate. WVG as a covariate had a significant or near-significant effect on the dependent variable in each analysis described below. WVG was not used as a covariate in the analysis of Clarity, however, as this variable did not have a significant effect on Clarity ratings. Pairwise comparisons reported are post-hoc tests on estimated marginal means after removing the influence of WVG. Significance levels were set at $p < .05$ for all tests.

3.2. Total Amount of Recalled Information

The total amount of information reported from Nap awakenings was unexpectedly low (Table 2). WIC was significantly lower for Nap reports relative to Late Morning reports, $t(38) = 2.21, p = .03, d = .49$, being instead comparable to WIC for reports from the Circadian Nadir (Figure 2). In addition, the percentage of participants who recalled any mentation at all when awak-

ened was lower during the nap period (40%) as compared to both Circadian Nadir (70%; $\chi^2 = 3.64, p = .057$) and Late Morning night NREM reports (70%; $\chi^2 = 3.64, p = .057$; Figure 2).

3.3. Other Mentation Characteristics

Mirroring the results for WIC, the Dreamlike Quality ratings of Nap reports were near-significantly lower than for Late Morning reports, $t(38) = 1.66, p = .10, d = .54$ (Table 2, Figure 3) but similar to the Dreamlike Quality of Circadian Nadir NREM reports ($p > .8$; Table 2, Figure 3). No other qualitative measures differed significantly across the diurnal cycle (Table 2).

The confounding influence of report length has been a considerable problem in dream research, as longer dreams tend to have, for example, a greater number of bizarre events merely by virtue of their greater length. When the influence of report length is controlled for in analyses of qualitative dream characteristics, some apparent qualitative differences between REM and NREM dreams have been found to disappear (Antrobus, 1983). Here, when additional analyses were conducted controlling for the influence of WIC as a second covariate, Dreamlike Quality, Bizarreness, Brightness, and Clarity did not differ significantly across the three report collection periods. Emotional intensity, however, demonstrated a near-significant tendency to be greater in Nap as compared to Late Morning reports, $t(38) = 1.75, p = .09, d = .57$, indicating that, despite the generally low amount of content reported from the nap, content which was recalled tended to be emotionally intense relative to that of night reports.

4. Discussion

Cortical and subcortical activation supporting cognition in sleep may be achieved via the heightened activation characteristic of REM sleep, but also occurs outside of REM, presumably via an alternative source of activation to the dreaming process (Antrobus et al., 1995; Cavallero, Cicogna, Natale, Occhionero, & Zito, 1992; Foulkes, 1967; Nielsen, 2000; Pivik & Foulkes, 1968; Solms, 2000). Here, hypothesizing that increases in NREM mentation across the night are due to circadian-driven increases in neural activity correlated with the CBT rhythm, we predicted that more mentation would be reported from a daytime nap as compared to periods of nocturnal sleep. Unexpectedly, nap reports demonstrated a relative paucity of mentation as compared

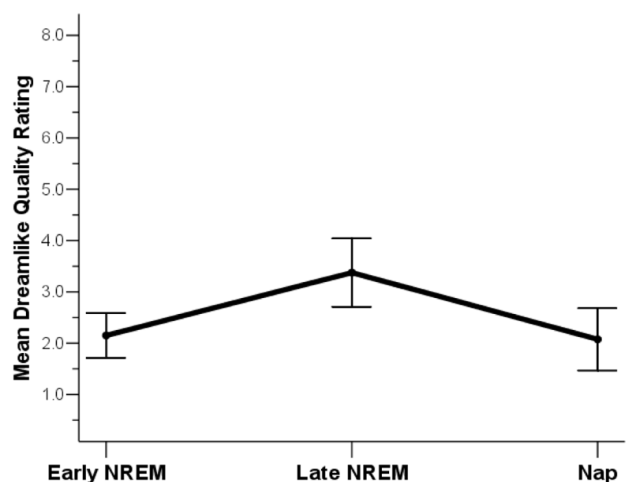


Figure 3. Dreamlike Quality ratings (\pm SE) for NREM reports across the diurnal cycle.

Table 2. Characteristics of Sleep Mentation Reports across the Diurnal Cycle.

	Circadian Nadir	Late Morning	Nap
% Recall	70%	70%	40%
Word Information Count (WIC)	3.7 ± 1.18	15.73 ± 5.23	7.15 ± 2.54
Dreamlike Quality	2.15 ± 0.44	3.38 ± 0.67	2.08 ± 0.61
Bizarreness	0.03 ± 0.03	0.4 ± 0.19	0.15 ± 0.09
Emotional Intensity	2.80 ± 1.07	3.10 ± 1.17	4.90 ± 1.72
Brightness	46.8 ± 8.92	39.13 ± 9.98	30.95 ± 8.83
Clarity	37.34 ± 7.45	31.56 ± 8.34	20.29 ± 6.18

Note. Means ± SE

to Late Morning reports collected after a night of sleep. Total amount of content reported from daytime naps, as measured by WIC, was instead similar to reports collected from NREM sleep near the nadir of the CBT rhythm. Admittedly, the present research questions might best be addressed using an entirely within-subjects design, and future studies should seek to compare overnight and nap mentation within the same subject group. However, here we demonstrate that the low mentation production observed in nap reports could not be accounted for by any of the most relevant individual differences between subject groups, including differences in WVG or trait dream recall.

The present findings cannot be explained by an exclusively circadian influence on dreaming correlated with the CBT cycle. Although our present data could be accounted for by a purely homeostatic-driven time course for dreaming, following changes in propensity for SWA across the day, this interpretation would be inconsistent with previous work demonstrating the presence of clear circadian effects on dreaming while controlling for time since sleep onset (Antrobus et al., 1995; Suzuki et al., 2004). Two general scenarios then present themselves as the most plausible accounts of our unanticipated results:

4.1. An Additive Influence of Circadian and Homeostatic Effects

Increased circadian activation during the early afternoon nap may have been counteracted by a concomitant increase in sleep need/SWA propensity. Since all subjects in the present study had relatively early habitual sleep phases, with an average wake time before 8:00am, participants were awake for approximately 4-5 hours prior to the experimental nap, providing ample time for the accumulation of sleep need and a concomitant increase in SWA propensity. It is unclear, however, what mechanism might account for an influence of SWA propensity on dream recall from stage 2 NREM sleep, where little slow wave activity is seen.

4.2. An Alternative Time Course for a Circadian Effect on Dreaming

We have presumed thus far that a circadian rhythm for dreaming might follow a time course similar to that of CBT, with a nadir several hours prior to habitual waking time and an acrophase in the early evening (Czeisler et al., 1990). However, a recent study employing an ultra-short sleep schedule forced desynchrony protocol provides evidence supporting a quite different time course for the circadian rhythm for dreaming (Suzuki et al., 2004), peaking at 8am and declining thereafter, mirroring the circadian rhythm for REM sleep propensity (Czeisler, Zimmerman, Ronda, Moore-Ede, & Weitzman, 1980). This timing is broadly consistent with the results we report here, though direct comparison of our data with that of Suzuki et al. (Suzuki et

al., 2004) is difficult due to widely divergent methodology. Our protocol specifically avoids introducing the term "dreaming" to participants and relies on detailed verbal reporting. Suzuki et al. (Suzuki et al., 2004), in contrast, restricted their mentation collection to having subjects rate "how much they dreamed" on a scale of 0-3 at each awakening. This expedient approach was certainly practical given their repeated nap design, yet such divergent methods of collecting dream reports are likely to have a profound influence on the resultant data. Specifically, the method employed by Suzuki et al. (Suzuki et al., 2004) may have resulted in a report collection method sensitive to detecting only more vivid, "REM-like" sleep mentation. In this case, it would not be surprising for the particularly long and vivid dreaming measured by Suzuki et al. (Suzuki et al., 2004) to correlate strongly with circadian fluctuation in REM propensity.

4.3. Dreaming in NREM and 'Covert' REM Sleep

Suzuki et al. (Suzuki et al., 2004) have interpreted their data as indicative that dreaming in NREM-exclusive naps is the result of "covert" REM processes (Nielsen, 2000). However, REM sleep is not the only biological function following an endogenous rhythm with an 8am peak, and consequently, an ~8am peak for dreaming in NREM does not imply that dreaming in NREM naps must be attributed to REM-related processes. The endogenous rhythm for cortisol, for example, follows a similar time course (Uchiyama et al., 1998), and given its known influence on memory encoding and retrieval (Andreano & Cahill, 2006; Buchanan & Lovallo, 2001), this neuromodulatory hormone provides at least as plausible an explanation for a late-morning peak in NREM dream recall as a mysterious influence of REM sleep on dreaming during NREM naps.

In the case of the present study, diurnal variation in REM propensity is a particularly unlikely explanation for the observed variations in dream reporting. Though close proximity to REM sleep may predict the report of mentation from NREM (Nielsen, 2000), we carefully controlled both nap and night awakenings such that mentation reports were always separated from the last REM period by at least 20 minutes. Additionally, NREM reports were not elicited when it appeared that subjects would shortly be entering a REM period. Studies of the influence of sleep architecture on dream reporting indicate that there is an increased likelihood of reporting dreaming from NREM when awakenings are made within 15 minutes of a REM period (Nielsen, 2000), a time period which we carefully avoided here.

4.4. Relationship of Current Findings to Previous Studies of NREM Naps

Although several previous studies have examined the characteristics of mentation during a brief diurnal nap (Benbadis, Wolgamuth, Perry, & Dinner, 1995; Islas-Marroquin & Delgado-

Brambila, 1998; Niedermeyer & Lentz, 1976; Palagini, Gemignani, Feinberg, Guazzelli, & Campbell, 2004; Taub, 1971), no study has previously compared laboratory-collected nap mentation to night mentation reports collected under similar conditions. Across studies, average recall of dreaming from daytime naps containing exclusively NREM has been 37.4% (Benbadis et al., 1995; Islas-Marroquin & Delgado-Brambila, 1998; Niedermeyer & Lentz, 1976; Palagini et al., 2004; Taub, 1971), a figure comparable to the 40% recall from NREM naps that we report here. Yet recall rates have varied widely, one study reporting that only 16% of subjects recalled any mentation (Niedermeyer & Lentz, 1976), and another 97% (Palagini et al., 2004). This variability seems to be related to substantially different methodologies for collecting dream content across these studies, as well as differences in definitions of 'dreaming'. Generally low figures for NREM nap recall (with the exception of Palagini et al., 2004) stand in stark contrast to anecdotal reports of long, vivid dreaming during daytime napping and the observation that vivid lucid dreams are more likely to occur during a late morning nap as opposed to at the end of a night of sleep (LaBerge, Phillips, & Levitan, 1994). Non-laboratory reports of intense or lucid nap dreaming could be due to the presence of REM sleep in longer naps, or to sleep fragmentation, a reported predictor of dreaming during NREM (Takeuchi, Miyasita, Inugami, & Yamamoto, 2001; Takeuchi, Ogilvie, Murphy, & Ferrelli, 2003).

5. Conclusions

Within-stage changes in sleep mentation across the night indicate the presence of sources of activation to the dreaming process other than the REM/NREM cycle. Understanding these processes is crucial to the study of cognition in sleep, inasmuch as we hope to identify its neural basis. The present study is the first to examine dreaming during daytime NREM naps in comparison to night reports, providing initial data on the relative contribution of homeostatic vs. circadian factors to changes in NREM mentation across the diurnal cycle. The low mentation production observed during early afternoon napping indicates that a purely circadian influence following the endogenous core body temperature rhythm is inadequate to explain diurnal variations in sleep mentation within NREM. Time-of-night effects on NREM mentation may therefore be due to either a) the combined influence of circadian and homeostatic factors or b) an exclusively circadian contribution to mentation reporting with an acrophase during the late morning hours (Suzuki et al., 2004). Future work addressing these questions should employ constant routine and forced desynchrony protocols, which are better able to parse circadian and homeostatic influences on sleep mentation.

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