Neurophysiological Evidence for the Detection of External Stimuli During Sleep

Kimberly A. Cote PhD,1 Lomega Etienne BA,2 and Kenneth B. Campbell PhD2

1Department of Psychology, Brock University, St. Catharines, Canada
2School of Psychology, University of Ottawa, Ottawa, Canada

Study Objectives: A cognitive evoked potential, labelled “P300,” is elicited when an observer attends to and detects an infrequently delivered “target” stimulus. It is not typically present if the target is ignored or undetected. P300 is therefore thought to reflect some aspect of consciousness of the stimulus. There has been much controversy concerning whether P300 can be recorded in sleep, a state in which information processing of external events is presumably reduced. The present study investigated the effects of both pitch and intensity stimuli on information processing, in order to determine whether a more salient stimulus might elicit a P300 in sleep that is comparable to the waking P300.

Design: A true P300 will have a parietal maximum peak following a rare stimulus, and its amplitude will vary inversely with the probability of stimulus delivery. Participants were thus randomly assigned to one of three probability groups, in which the deviant was presented on 20%, 10%, or 5% of trials.

Setting: Data were collected in the Human Neurophysiology Laboratory at the University of Ottawa.

Participants: Twenty-four young adults.

Interventions: N/A

Measurements and Results: During wakefulness, a parietal P300 was apparent following both pitch and intensity deviants when participants were asked to detect deviant stimuli. A P300 was also apparent following the intensity deviant when participants were instructed to ignore the stimuli. During non-REM sleep, no P300 could be identified. In REM sleep, very rare (p=.05) loud deviants elicited a parietal P300. This P300 was attenuated relative to the waking ignore condition. Moreover, the frontal dispersion of the peak was absent.

Conclusions: These data provide evidence that participants are conscious (parietal P300) of very rare and intrusive stimuli during REM sleep, although the frontal aspects associated with this consciousness may be absent.

Key words: Sleep, consciousness; attention; event-related potentials; P300; REM sleep; information processing

INTRODUCTION

ONE OF THE GREAT PUZZLES OF SLEEP IS THE EXTENT TO WHICH THE SLEEPER IS AWARE OF EVENTS IN THEIR EXTERNAL ENVIRONMENT. Information processing capabilities at sleep onset and across various depths of sleep are of interest to a general audience, including psychologists, philosophers, and those in the medical field (particularly anesthesiologists). Awareness during sleep is relevant for studies of sleep maintenance in good and poor sleepers, the effects of environmental noise on sleep quality, and memory and learning during sleep. The extent of such information processing and consciousness during sleep has been debated for some time. One view is that awareness of external events is not possible, particularly during REM sleep when mental resources are focused toward internal dream activity.1 On the other hand, in the case of lucid dreaming, consciousness must be possible in order for the sleeper to be aware of their dreams and to subsequently signal to the experimenter that they are dreaming.2 Investigating information processing during sleep may also further our understanding of functions of sleep. For instance, Snyder’s sentinel theory proposed that REM sleep served to periodically prepare the brain for arousal in the event that the sleeper might need to respond to threatening stimuli (e.g., predators) in the environment.3

Although data did not support this theory (i.e., prey species did not have more REM sleep than their predators), it may be that enhanced information processing capabilities in REM sleep may be needed or may have developed to provide sensory stimulation to the brain over a long period of continuous non-REM sleep. This position is in line with the view that REM sleep is more like a state of wakefulness than sleep. Indeed, REM sleep is similar to the waking state in many respects.

A major difficulty encountered in the study of awareness during sleep is that the experimenter does not have direct access to the sleeper’s mental state. For instance, the sleeper is usually unable to provide either a verbal or behavioral response. Thus, even if the sleeper is conscious of the external environment, he or she may be unable to signal awareness to the experimenter. It is, of course, possible to awaken the subject and ask him or her to recall mental activity. The reliability of such subjective recall is questionable. A failure to recall events immediately prior to awakening may reflect a failure of memory storage or retrieval rather than a lack of awareness of the external stimulus.4 Event-related potentials (ERPs) offer a means to probe the extent of information processing during sleep, independently of subjective reports or behavioral responses. The long-latency auditory ERPs are particularly affected by manipulation of the subject’s level of attention, arousal, and consciousness.5-9

The vertex complex of the ERP consists of an “N1” (negative wave peaking between 80-100 ms) and a “P2” component (positive wave peaking between 175-225 ms). Näätänen2 has suggested that N1 may act as a transient-detector system that triggers an internal attentional system. N1 may subserve “conscious perception of auditory stimuli in general. . . without indicating what the stimulus is or what its precise features are” (p.212). As might be
expected by a measure of “general consciousness,” N1 is attenuated to near baseline level in non-REM sleep compared to wakefulness. During REM sleep, N1 returns to about 25%—50% of its waking amplitude.9 There is thus some evidence that a general type of conscious perception may remain possible in REM sleep.

In the oddball task, participants are presented with a train of frequently occurring standard stimuli. At rare and unpredictable times, the standard is changed to a deviant. When participants are asked to actively detect the rare deviant stimulus, a late positive potential is elicited.10 When the deviant is easy to detect, it peaks at about 300 ms. It has thus been labelled “P300”. P300 is maximum over parieto-central areas of the scalp. It only occurs when the deviant stimulus is actually detected. It will not be elicited if the subject ignores the stimulus or fails to detect it. The P300 is therefore thought by many authors to reflect consciousness of the deviant stimulus.8

In earlier reviews, Campbell et al.6 and Harsh11 both claimed that there was no convincing evidence that a P300 could be recorded in sleep. Some studies have reported a late positivity in sleep. Nevertheless, this late positivity may not be equivalent to a P300. In some cases, the P300 was not larger to the rare stimulus.12-13 In others, its latency was too long or its scalp topography did not correspond to the classic parietal maximum P300.14-16 More recent studies have provided evidence that P300 can perhaps be elicited in REM sleep. Researchers from Japan17 and France13 employed oddball tasks in which the pitch of a frequently occurring standard stimulus was changed on 20% and 10% of trials respectively. Both groups reported a small amplitude P300 during REM sleep. Cote and Campbell18 subsequently investigated whether this P300 was a result of the loud, intrusive nature of the stimulus or its extreme infrequency of occurrence. Stimuli of various intensities (0, 60, 80 or 100 dB SPL tone pips) were presented at an equal probability of occurrence. Only the loudest stimulus elicited a P300 in REM sleep.

The purpose of present study was to determine whether or not a true P300 could be elicited in sleep. This was accomplished by examining the effects of both pitch and intensity deviants on P300 in sleep in the same participants. A classic manipulation known to affect a true P300 is to change the probability of deviant occurrence. P300 amplitude increases as the probability of deviant occurrence decreases.20-21 The probability of deviant occurrence was therefore manipulated. Different odd-ball tasks were presented, during which rare stimuli were delivered on either 20%, 10%, or 5% of trials respectively. P300 can usually only be elicited when participants actively detect the rare deviant stimulus. Thus, a pitch deviant will only elicit a P300 if participants attend to and detect it. An exception to this rule is for very loud stimuli. They will elicit an obligatory P300 in waking and alert participants even if the participants are not attending to the stimuli.22-25 Waking data were therefore also collected when participants were attentive to the auditory stimuli and when they ignored them.

METHODS

Participants

Participants were 24 (16 female) volunteers, aged 18 to 30 years (M=23.3, SD=3.8). They signed a consent form and received an honorarium for their participation. All participants completed a series of sleep/wake questionnaires and had a hearing test prior to study. Hearing levels were verified to be within 15 dB ISO at 500, 1000, 1500 and 2000 Hz. All participants were good sleepers, right-handed, non-smokers, and free from medication at the time of study. None had a history of psychiatric or neurological disorders. Instructions were given to abstain from alcohol and caffeine on the day of the study.

Physiologic Recording

The EEG was recorded from midline frontal, central, parietal, and occipital scalp sites (Fz, Cz, Pz, and Oz) and referenced to the left mastoid. A vertical EOG was recorded between the supra- and infra-orbital ridge of the right eye. A horizontal EOG was recorded from submental electrodes. A ground was placed on the forehead. Inter-electrode impedance was below 5 kOhm. The high filter for the EEG and EOG channels was set at 35 Hz, while the EMG was set to 120 Hz. The time constant was set at one second for the EEG and EOG channels, and at 0.03 s for the EMG. All physiological data were sampled continuously at 256 Hz using a 12-bit A-D converter and stored on hard disk.

Procedure and Stimuli

Participants arrived to the laboratory at approximately 19:00 in order to allow time for electrode application procedures and waking data collection. Each participant was fitted with a hearing-aid device in the right ear through which the auditory stimuli were presented. The hearing-aid device assured constancy of auditory input in spite of variations in head movement.

Participants were presented with auditory stimuli during wakefulness and throughout the night during all stages of sleep. An 80 dB SPL, 1000 Hz stimulus was delivered on average every 1.5 seconds. The inter-stimulus interval (ISI) varied at random from 1000 to 2000 ms. Total stimulus duration was 52 ms, with an abrupt 2 ms rise-and-fall time. In different conditions, the standard was changed at rare and unpredictable times to either a high pitch (2000 Hz), or a loud intensity (100 dB SPL) deviant. Participants were randomly assigned to one of three probability groups in which the probability of deviant occurrence was either .20, .10, or .05. A between groups design was employed to avoid possible carry over/ habituation effects that might occur in a within groups, repeated measures design. The number of participants in the .20, .10, and .05 deviant probability groups was 7, 7, and 10, respectively.

During wakefulness, participants were asked to either attend to (and count the deviant) or ignore (and read a book) the stimuli in different conditions. Accuracy of the mental count was subsequently verified. Stimuli were presented in blocks of 400 trials. The order of presentation of conditions was randomized. All conditions were presented at least two times while awake and in each stage of sleep to ensure reliability of results.
Data Analysis

The continuous EEG was classified by an experienced rater using standard sleep scoring criteria based on 15 second epochs. In the case of stage ambiguity, movement arousals, or the presence of stage 1 sleep, the data were excluded from further analysis. Stages 3 and 4 were combined to form slow-wave sleep (SWS). Stage 2 was sub-divided into early and late halves of the night to examine for possible time-of-night differences. REM sleep was divided into tonic and phasic epochs on the basis of eye movements. A method similar to that described by Sallinen and colleagues was employed—REM sleep was characterized as “tonic” if no rapid eye movements occurred during the 10 second interval prior to the onset of the deviant, or the five seconds interval following it. If there was at least one eye movement in the five seconds prior to the onset of the deviant, the trial was classified as “phasic.” In the present study, tonic trials included those with no REMs occurring six trials prior to or four trials following the deviant (i.e., on average, nine seconds prior to and six seconds following the deviant). Phasic trials were those with at least one REM in the four trials prior to the onset of the deviant. If an eye movement occurred within four trials following the deviant, but not before it, the REM interval was classified as neither phasic nor tonic. These trials were rejected from further analysis.

Data were reconstructed off-line into discrete trials or “sweeps”. A sweep consisted of 256 data points beginning 100 ms prior to stimulus presentation and continued for 900 ms following it. During wakefulness, trials in which the EOG or EEG exceeded ±100 µV were rejected from further analysis. Within sleep, trials were rejected if the EEG exceeded ±100 µV. During stage 2, these rejection criteria essentially removed trials in which the stimulus elicited a K-Complex. The K-Complex will be elicited on 25%—50% of deviant presentations. The large negative component of the K-Complex, peaking at about 500-600 ms overlaps and summates with earlier positive waves, possibly masking a P300. Within REM sleep, the rejection criteria removed trials with abnormally high amplitude EEG. Since the rejection criteria were not applied to the EOG channels, trials in which rapid eye movements occurred were not rejected. The EOG artifact (phasic eye movements) is not, however, time-locked to the stimulus (i.e., it occurs randomly). The averaging procedure, summatint both negative- and positive-going EOG activity, should tend to cancel out the random eye movements.

Trials were sorted and averaged on the basis of sleep stage (stage 2, SWS, REM sleep), stimulus type (pitch, intensity), and deviant probability (.20, .10, .05). They were later digitally filtered (an inverse FFT algorithm operating in the frequency domain) using a 15 Hz high frequency filter.

Determining if a P300 exists in sleep is fraught with statistical and technical difficulties. A simple approach would be to compare the waking and sleeping P300s. However, a failure to find a difference does not imply the presence of a sleeping P300. For example, it is quite possible that there may not be a P300 in the ignore condition in the waking state. Similarly, a difference between waking and sleeping amplitudes of P300 does not imply the absence of P300 in sleep.

Previous research has indicated that a pitch-elicited P300 may not be elicited in wake-ignore conditions, nor within non-REM sleep. For statistical purposes, a waveform in which no P300 is apparent still needs to be quantified. This was accomplished using a data-point averaging technique. Each standard and deviant...
waveform sweep in all conditions was divided into five equal time interval windows beginning 250 ms and ending 500 ms following stimulus onset. All data within the following intervals were averaged: interval 1=250-300 ms; interval 2=300-350 ms; interval 3=350-400 ms; interval 4=400-450 ms; and interval 5=450-500 ms. Initially, the presence of a candidate P300 was determined by comparing the standard and deviant waveforms across each of the five intervals using the paired t-test statistic. Separate t-tests were run for the attend and ignore conditions within the waking state and within each stage of sleep, for the pitch and intensity conditions within each probability group. It was expected of course that a P300 would be larger (i.e., more positive), following the rare deviant than the standard stimulus. Because a positive directionality was predicted (i.e., the polarity

Figure 2—ERPs following intensity deviants and standards in wake—attend condition. Again, the P300 is largest in the rarest probability condition (p=.05) and decreases in amplitude with increasing probability of the deviant. P300 amplitude following the intensity deviant is larger than that following the pitch deviant.

Figure 3—ERPs following pitch deviants and standards in wake—ignore condition. No P300 is apparent in any condition.
of P300), a one-tailed test of significance (p<.05) was applied.

The use of such multiple tests will of course likely increase Type I error and result in chance significance. This liberal statistical approach was used to demonstrate that significant differences could not be found in many of the comparisons. These preliminary analyses were followed with more precise measurement of the P300 waveform and conservative statistical analyses among stages and/or conditions. When the t-test comparing the standard and deviant waveforms was significant, the peak amplitude of P300 was measured at Pz in the deviant ERP as the maximum positive peak between 250 and 500 ms. The amplitude and latency of the deviant ERP were then compared using ANOVA procedures.

RESULTS

Waking ERPs

Figures 1, 2, 3, and 4 illustrate the standard and deviant ERPs during wakefulness in the attend and ignore conditions for the pitch and intensity conditions respectively. In wakefulness, across all conditions, the standard N1 peaked at about 75 ms. A double-peaked P2 was apparent, with an initial peak at 140 ms and a later peak at 205 ms. The amplitude of the standard N1 did not vary among the three probability groups. The type of deviant (i.e., pitch, intensity) did not affect the amplitude of N1. N1 was slightly reduced in amplitude in the ignore conditions, compared to attend conditions, but this difference was not significant.

Table 1 presents the results of the 60 t-tests run to compare the standard and the deviant ERPs in the waking state. When participants were asked to count the number of deviant presentations, in both the intensity and the pitch conditions for all probability groups, the deviant ERP was significantly more positive-going than the standard over all intervals from 250 to 500 ms. The results were quite different when participants ignored the auditory stimuli. When the pitch deviant was employed, the standard and the deviant waveforms did not significantly vary in any of the five time intervals, among any of the probability groups. When the intensity deviant was employed, significant differences were found among the standard and deviant ERPs when the deviant occurred infrequently (.10 and .05 groups). No significant standard-deviant differences were found when probability of deviant occurrence was .20. ANOVA procedures were restricted to those conditions in which the P300 was apparent.

A Group (3 probability conditions) by Deviant (pitch versus intensity) by electrode Site (Fz, Cz, Pz, Oz) repeated measures ANOVA was run to compare P300 latency and amplitude data in wakefulness during the attend condition. The latency of P300 was significantly earlier following the intensity (M=316 ms) compared to the pitch deviant (M=355 ms), at all electrode sites, F(1,21)=11.40, p<.0001. A significant main effect of type of deviant was also found for the amplitude of P300, F(1,21)=46.65, p<.0001. P300 amplitude was larger following the intensity (M=22.8 V) compared to the pitch deviant (M=6.53 V). There was a trend toward differences among the three probability groups, F(2,21)=2.97, p<.07. P300 was largest when probability of deviance occurrence was .05 (M=11.50 V) and declined in amplitude in the .10 and .20 conditions (Ms=8.77 and 6.60 V, respectively). There was also a highly significant main effect of electrode site, F(3,63)=57.79, p<.01. P300 was largest at Pz (M=13.45 V). Its amplitude remained large at both Cz (M=10.67 V) and Oz (M=8.12 V). It was much smaller in amplitude at frontal sites (M=3.60 V).
### Table 1—One-tailed t-test comparisons of standard vs. deviant stimuli in wakefulness

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The p-values are underlined for differences that were significantly more positive.
### Table 2—One-tailed t-test comparisons of standard vs. deviant stimuli in sleep

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<th>p</th>
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The p-values are underlined for differences that were significantly more positive.
Figure 5—ERPs following intensity and pitch deviants in stage 2 non-REM sleep. No P300 can be observed in any condition. A positive peak is apparent in the 400 - 450 ms range at occipital sites and it is largest for the rarest probability condition. This could be due to a limited number of small amplitude (less than 100 V) K-Complexes present in the average.

Figure 6—ERPs following intensity and pitch deviants in REM sleep. P300 is visible following the intensity deviant in the rarest (p=.05) probability condition only. It is not visible at fronto-central sites. In the .20 and the .10 probability conditions, the ERP waveform is characterized by large amplitude P1 and P2 peaks, followed by a late slow negative wave. Note that this and all other figures of REM data are displayed at double the amplitude.
Figure 7. ERPs following the pitch deviant in tonic vs. phasic REM sleep. Note that N1 tends to be smaller and P2 larger in tonic REM.

Figure 8. ERPs following the intensity deviant in tonic vs. phasic REM sleep. Again, note that N1 tends to be smaller and P2 larger in tonic REM.
In the ignore condition, as mentioned a significant P300-like wave was not apparent following the pitch deviant regardless of its probability of occurrence. Candidate P300s were identified following the intensity deviant when the probability of occurrence was .10 or .05. To further investigate the effects of attention on the waking P300, an ANOVA was run to compare the attend and ignore conditions for the intensity deviant. The peak latency of P300 in the ignore conditions was 315 ms. It did not significantly differ from the attend conditions (F<1). A main effect of attention on P300 amplitude was observed. P300 amplitude was significantly larger in the attend (M=13.21 V) compared to the ignore condition (M=5.77 V), at all electrode sites and for both the .10 and .05 probability conditions, F (1,15)=139.73, p<.10-5. Again, although P300 was largest at Pz, its remained apparent at all sites.

Non-REM Sleep

There was insufficient data from SWS to permit reliable averaging. This may have been because external stimuli, especially those that are loud, can reduce the amount time spent in SWS. Non-REM data were therefore reported for stage 2 sleep only. There were no time-of-night differences apparent in the grand average waveforms. ERPs were therefore collapsed across the entire night. In stage 2 non-REM sleep across all conditions, the latency of the standard N1 was prolonged to approximately 110 ms, while P2 peaked at approximately 200 ms. The amplitude of N1 was at or below baseline while P2 increased in amplitude in all conditions relative to wakefulness.

Figure 5 superimposes the pitch and intensity deviant ERPs within stage 2 sleep. A late positivity was not apparent following the pitch deviant regardless its probability of occurrence. When the intensity deviant was employed, a large, negative wave peaking at about 650 ms was apparent over frontal and central sites. At parietal and occipital sites, a small amplitude positive wave was apparent around 421 ms, particularly for the most rare deviant condition. The upper portion of Table 2 shows the results of the t-tests comparing standards and deviants for the pitch and intensity conditions at all levels of probability. No significant differences were observed between the standard and the deviant ERPs waveforms in any of the intervals between 300 and 500 ms.

REM Sleep

In REM sleep across all conditions, the standard N1 and P2 peaked at about 110 and 180 ms respectively. N1 was reduced in amplitude by approximately 25%—33% compared to the waking state. Figure 6 superimposes the pitch and intensity deviant ERPs in REM sleep across the three probability conditions. This P300 was maximum at Pz. Unlike the case in the waking conditions, its positivity was not apparent at the Fz site. Rather a very large negativity was observed here.

The lower portion of Table 2 provides the results of the t-tests comparing the standard and deviant ERPs in REM sleep for the pitch and intensity conditions at each level of probability. Again, no significant differences were apparent in the 300 to 500 ms intervals when a pitch deviant was employed, regardless of its probability of occurrence. When the loud, deviant was employed, the deviant waveform was significantly different from the standard in the four intervals ranging from 300 to 500 ms, but only when deviant occurrence was extremely rare (p=.05).

There was no evidence of a P300 following the loud deviant when the probability of occurrence was either .10 or .20. The P300 following the loud deviant in the .05 probability group was therefore analyzed further. P300 peak latency was not significantly different in REM compared to the waking-ignore condition (365 and 315 ms respectively). A one-way ANOVA run on P300 amplitude at Pz indicated that it was significantly larger in the wake-ignore condition (M=10.74 V), than in REM sleep (M=5.36 V), F(1,9)=45.10, p<.0001.

A late large amplitude negative slow-wave (SW) was observed over parieto-occipital sites. It peaked at approximately 600-850 ms. It was larger following the intensity than the pitch deviant at occipital sites across all probability levels.

REM sleep was further investigated by sorting trials into phasic and tonic epochs. This sorting was done because it is possible that averaging over the entire REM period could have obscured intra-REM differences. In general, there were more phasic than tonic epochs of REM in the analysis. A Group (3 probability conditions) by Deviant (pitch vs. intensity) by REM State (tonic vs. phasic) repeated measures ANOVA was run at each electrode site separately. At Cz, a main effect of REM state was observed for the amplitudes of N1 and P2. N1 was reduced in tonic REM, but the difference did not reach significance, F(1,21)=3.13, p<.09. The amplitude of P2 was significantly larger in tonic REM at Fz and Cz, F(1,21)=5.28, p<.01. There were no significant interactions involving N1 and P2.

A P300 was still not apparent in either tonic or phasic REM when a pitch deviant was employed. Similarly, a P300 was not apparent in either tonic or phasic REM when the probability of occurrence of the loud deviant was either .10 or .20. P300 was, however, visible in both tonic and phasic REM to the very rare intense deviant. The amplitude of this P300 did not significantly vary between tonic and phasic REM states, F<1. The latency of P300 was prolonged during tonic REM, but the difference was not significant, F(1,9)=2.41, p<.15.

The late SW did not show consistent differences between tonic and phasic REM. The SW tended to be larger in tonic REM when the probability of deviant occurrence was high (.20) and to be larger in phasic REM (particularly for the intense deviant), when probability of deviant occurrence was low (.05). There was however wide inter-subject variability.

DISCUSSION

The standard stimulus elicited the usual N1-P2 waveform. The physical characteristics of the standard did not vary in either the pitch or the intensity conditions. During the waking state, it was not affected by the type of deviant stimulus nor the probability of deviant occurrence. N1 was slightly reduced in amplitude when participants were awake and alert but ignoring the auditory stimulus, compared to when they were attending to them. The attend-ignore difference was however not significant. Stimuli that are presented at rates slower than every one second are difficult to ignore. As a result, N1 may not be affected by manipulation of the subject’s direction of attention.31 N1 was consistently at or below baseline while P2 increased in amplitude during stage 2 sleep. This also replicates many previous studies.6,12,29,32-34 During stage REM, the amplitude of N1 and P2 occupied an intermediate position between the waking state and stage 2.
In wakefulness, the oft-reported effects of attention were observed on P300 amplitude. When participants counted the deviant stimuli, P300 became larger as its probability of occurrence decreased. This is consistent with the classic study by Duncan-Johnson and Donchin.20 P300 was significantly larger to the loud, intense stimulus than to the pitch deviant. This appears to contradict the well-documented endogenous nature of P300. Many authors report that P300 is unaffected by the physical characteristics of the stimulus. It is quite possible that this apparently exogenous effect might be due to an endogenous confound—the ease of detection of the loud deviant. Deviants that are easier to detect may elicit larger amplitude P300s than those that are difficult to detect.8

A parietal maximum P300 was observed whenever participants were asked to actively detect the deviant stimulus. When participants were asked to ignore the stimulus, there was no P300 to the pitch deviant, even if it occurred very rarely. When the deviant was very loud and very rare (.10 and .05), a P300 was elicited in the ignore condition. This is consistent with previous research which showed that an obligatory P300 may be elicited in wake—ignore conditions when stimuli are sufficiently loud.22-25 This is presumably because very intense stimuli intrude into consciousness since participants are not able to inhibit the processing of them. In both the attend and ignore conditions, it appears that a P300 will be elicited whenever the subject becomes conscious of the deviant stimulus whether this consciousness is internally or externally controlled. The amplitude of this P300 was widespread, remaining large at both Cz and Fz in the waking conditions.

In stage 2 sleep, there were no significant differences between the standard and deviant waveforms in any of the intervals between 300 and 500 ms for either the pitch or intensity deviant at any probability of occurrence. Therefore, even when very liberal multiple one-tailed t-tests were employed, a significant P300-like wave could not be found in stage 2 sleep. Failure to observe a P300 on the scalp does not necessarily mean it did not occur. At frontal and central sites, a large, late negativity peaking at about 650 ms was observed. Rare, salient stimuli will elicit unique sleep-related waveforms, including two negative polarity peaks, occurring at about 350 and 550 ms. The N550 appears to occur only when the K-Complex is elicited. Our averaging procedure rejected any large amplitude (exceeding 75 V) K-Complexes. Nevertheless, on single trials, it is possible that some smaller amplitude K-Complexes (or the summation of background noise and the K-Complex) might not have been rejected. The N350 also occurs when the K-Complex is elicited but can also occur independently of it.28 Its amplitude is considerably smaller than the N550 and as such, would not have been rejected during averaging. The very large amplitude N550 is maximum over fronto-central areas of the scalp although it is also propagated in more posterior regions.35-36 The N350 is maximum over central areas of the scalp and may be identical to the sleep-related vertex sharp wave.37 A late parieto-occipital positive peak was visible in the grand averaged waveforms following the rare, intense deviant. It peaked at about 420 ms. This late deviant positivity was, however, not statistically different from the standard waveform data in the 400 to 500 ms interval. It peaked too late and its scalp distribution was more occipito-parietal than the usual parietal P300.18-30 A similar posterior maximum positive peak has also been observed in stage 2 in a number of other studies.14-16, 18, 30,38-40 The failure to observe the usual parieto-central P300 scalp distribution could, of course, be due to the overlapping and summing effects of the large fronto-central stage 2 negativity. These late negativities do not occur in either the waking state or in REM sleep, allowing the “true” P300 to emerge.

In REM sleep, there was no evidence of a late positive wave following the pitch deviant regardless of how infrequently it was presented. The failure to find a REM P300 when the pitch deviant was employed is consistent with the often observed failure to elicit it in the waking state when participants ignore the stimuli. The results are however inconsistent with reports by Niiyama et al.17 and Bastuji et al.,13 who did observe a small amplitude positive wave in REM sleep following pitch deviants. Both Niiyama et al.17 and Bastuji et al.,13 and the present study, employed brief duration 1000 Hz standard and 2000 Hz deviant stimuli. The rate of presentation was quite similar. The probability of deviant occurrence was .20 in the Niiyama et al.17 study. They could not observe a P300 in the actual deviant ERP. However, when the standard and deviant ERPs were subtracted, a small amplitude parieto-occipital positivity occurring at about 361 ms was visible in the difference wave. This subtraction procedure is equivalent to running a t-test to compare the standard and deviant waveforms. In the present study, no significant differences were apparent in the 300 to 500 ms range when the probability of deviant presentation was .20. Bastuji et al.13 delivered pitch deviants on 10% of trials. They noted a late (445 ms), small (3.6 V) positivity following the deviant in REM sleep. This is an unusually late for a “true” P300. In the present study, a similar late positivity could not be observed in the .10 deviant probability condition. It is possible that only the intensity deviant elicited the P300 in the present study because it was the most salient of the two types of stimuli being delivered. That is, the sleeper was presented both intensity and pitch stimuli within a single night. It seems reasonable that any within subject design employing multiple stimuli may lead to the P300 being elicited following the most relevant or meaningful stimulus.

The very rare loud deviant did elicit a parietal P300 in REM sleep. This P300 was significantly reduced in amplitude compared to that observed in the waking-ignore condition. The more frequently occurring intensity deviants did not elicit the P300 in REM sleep. It is possible that the failure to observe a significant P300 in the .10 and .20 deviant probability condition was due to the smaller number of participants in these groups compared to the .05 condition. This is unlikely. During REM, the ERPs following the loud deviant were actually more negative going than following the standard in the 300-500 ms interval for the .10 and .20 groups. Only very loud and very rare stimuli will elicit the REM P300.

Most ERP sleep studies have employed relatively simple acoustic stimuli such as pure tones. Perrin et al.38 presented eight different spoken names to sleeping participants. One of these was the subject’s own name. This procedure elicited a P300 waveform in REM sleep. Its amplitude was reduced by approximately 50% in REM compared to the wake—ignore condition. Pratt, Berlad, and Lavie,40 also presented the subject’s own name during sleep, but did not observe a P300 in REM sleep following this relevant stimulus. Perrin et al.38 point to methodological differences between the studies which may account for the discrepant findings. Specifically, in the study by Pratt et al.40 a single “other” name was employed as the standard stimulus, while the study by...
Perrin et al.18 presented a total of seven “other” names. It would therefore appear that both simple and complex stimuli will elicit a P300 in REM sleep providing they occur very infrequently and are either psychologically or biologically relevant. Perrin et al.39 also noted that the subject’s own name would also elicit a P300 during NREM sleep. Its scalp topography was largest over parieto-central areas of the scalp. Again, a large, large frontal-central negative wave, perhaps associated with the K-Complex did tend to overlap and summate with this late positivity.

In present study, P300 was not apparent at the frontal site in REM sleep. This was also the case in Cote and Campbell,19 Bastuji et al.,13 and Perrin et al.38 Bastuji et al.13 reported a negative-going wave at Fz at about 330 ms. In the present study, a large amplitude frontal negativity was also visible over frontal sites in the 300 to 400 ms time period in REM sleep. The parietal P300 might be involved with contextual updating of memory following the detection of the deviant. The role of frontal activity in the generation of P300 remains largely unknown. Frontal lobe patients show a parietal P300 following the presentation of novel stimuli but the frontal P300 to these same stimuli is absent.41 It is possible that the frontal contribution to P300 is also absent in REM sleep. There is evidence of frontal disconnection during REM. For example, neuroimaging studies have shown that there is significant deactivation in the prefrontal cortex during REM sleep.1 In terms of consciousness, it is possible that participants may be able to make conscious detections (parietal P300) during REM sleep, but not “experience” this consciousness (absence of frontal P300). This may also explain why participants do not awaken following apparent detection of the loud, intrusive deviant or their own name. There is some evidence nevertheless that P300 might more accurately reflect pre-consciousness. In the case of cortical blindness patients engaged in a visual oddball task, they are not able to overtly signal detection of the target. However, P300 is still elicited.

The late negative SW in REM sleep has also been observed previously.18,19,40,42 In previous reports, we suggested that this SW may be related to PGO activity, since it had an occipital-dominant scalp distribution, accompanied eye movements in REM, and was sensitive to changes in stimulus intensity. In the present study, the SW was again larger to more intense stimuli. There were no consistent differences in the amplitude of this SW between phasic and tonic REM trials across the various probability conditions. Cote and Campbell19 observed SW to be larger on phasic trials, but a single intense deviant, whose presentation was very rare, was employed. In the present study, when the intense deviant was presented on only 5% of trials, the SW was again largest on phasic trials. While the SW may be large to very rare intense deviants during phasic REM, there is little consistency with other probabilities or with the pitch deviant.

Sallinen, Kaartinen, and Lyytinen27 suggested that there might be more extensive information processing during tonic than phasic REM. This is because participants’ attention may be directed to internal mental activity (dreaming) during phasic REM. There was little support for this theory in the present study or in Cote and Campbell.19 N1 was consistently larger and P2 smaller during phasic compared to tonic REM. The increase in N1 and the decrease in P2 can be explained by the effects of an overlapping attentional waveform, Processing Negativity (PN). PN overlaps and summates with both N1 and P2, causing N1 to become larger (i.e., more negative), but P2 to become smaller (i.e., less positive or more negative). PN is thought to reflect the additional processing that an attended channel receives.7 This explanation is at odds with that of Sallinen et al.27 Participants appear to be more attentive to the external environment during phasic REM. In support of this, P300 latency was prolonged during tonic REM. Stimulus classification therefore takes longer during tonic REM. The amplitude of P300 was however not affected by the different types of REM. Differences between phasic and tonic REM therefore occur relatively early in information processing (at the time of N1) rather than at the stimulus classification stage of processing.

It is perhaps surprising to some, in light of arousal thresholds studies, that P300 would be elicited in REM sleep but not non-REM sleep. Specifically, it has been demonstrated that sleepers are more easily awoken from non-REM sleep. Does this increased chance of response indicate that there is greater information processing in non-REM sleep? We have argued that the presence of a P300 indicates an extensive level of cognitive processing involving stimulus discrimination and perhaps even consciousness. This is not to say that information processing does not occur in non-REM sleep. Obviously, one can awaken a sleeper from non-REM quite easily, with a gentle touch, the call of the sleeper’s name, or an alarm clock. The sleeper is thus able to process meaningful information in non-REM sleep. If the presence of a P300 in REM sleep indicates that more extensive processing is taking place, why then is it more difficult to arouse the sleeper from REM? It is possible that other unique evoked potentials, such as the vertex sharp wave or the K-Complex serve an information processing role in non-REM sleep. Neither occurs in REM. Moreover, one of the hallmark features of this paradoxical state is muscle atonia. REM sleep is also associated with more intense mental imagery. It is perhaps the presence of such muscle atonia, or the enhanced degree of attention to internal stimuli (dreaming), that prevent the sleeper from awakening, despite the enhanced cognitive processing of the external stimulus event. Nevertheless, the presence of a waking-like P300 in REM sleep, but not in non-REM sleep, provides neurophysiological evidence of enhanced information processing capabilities in REM sleep.

Conclusion
Current evidence suggests that either rarely presented biologically relevant (e.g., loud tones),18,19 or psychologically relevant stimuli (e.g., the subject’s own name),38,40 are necessary to elicit the parietal P300 during REM sleep. Such salient stimuli may be detected by the sleeper in REM, but not non-REM sleep. The absence of P300 at frontal sites in REM sleep may be the result of frontal deactivation that is characteristic of REM sleep.1 It is perhaps the lack of frontal contributions to consciousness that allow the sleeper to detect the stimulus, yet prohibit the sleeper from awakening to respond.

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