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# Processing of auditory stimuli during tonic and phasic periods of REM sleep as revealed by event-related brain potentials

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**SUMMARY** The brain has been reported to be more preoccupied with dreams during phasic than during tonic REM sleep. Whether these periods also differ in terms of the processing of external stimuli was examined. Event-related brain potentials (ERPs) to a frequent standard tone of 1000 Hz ($P=97\%$) and infrequent deviant tones of 1100 and 2000 Hz ($P=1.5\%$ for each) were recorded ($n=13$) during wakefulness and nocturnal sleep. An ERP wave (called REM-P3) resembling a waking P3 wave was larger for the 2000 Hz deviant during tonic than during phasic REM sleep. Also the P210 wave was larger during tonic than during phasic REM sleep. A reliable mismatch negativity component appeared only in wakefulness. In summary, these results support the hypothesis that the brain is more 'open' for changes in an auditory input during tonic than phasic REM sleep.

KEYWORDS auditory stimuli, event-related potentials, phasic, REM sleep, tonic

## INTRODUCTION

Rapid eye movement (REM) sleep is known to contain phasic and tonic periods (Moruzzi 1963). Phasic periods are characterized by bursts of REMs whereas no REMs occur during tonic periods. Several studies have shown that these two periods of REM sleep differ in terms of mental state to some extent. Subjects' dreams have been found to be more active (Berger and Oswald 1962; Pivik and Foulkes 1966; Firth and Oswald 1975) and emotionally more intense (Dement and Wolpert 1958; Karacan *et al.* 1966) when they have been aroused from a phasic REM sleep period than from a tonic period. Subjects have also had a stronger feeling of immersion in a sleep mentation experience after a phasic REM sleep awakening (Weinstein *et al.* 1988). In addition, a study by Taylor *et al.* (1985) suggests that a burst of REMs is associated with an orienting response to dream content. Thus it seems that the brain is more preoccupied with the ongoing mental activity during phasic than during tonic REM sleep.

A question of interest is whether phasic and tonic REM sleep periods also differ in terms of processing of external events. Price and Kremen (1980) showed that the behavioural response threshold for auditory stimuli is higher during phasic REM sleep than during tonic REM sleep. In their study, the subjects were instructed to press a microswitch once when they detected a 450 Hz tone and twice when they heard a 600 Hz tone. The more intense stimuli were needed to elicit the behavioural response during phasic than during tonic REM sleep. No difference was found in the ability to discriminate between tones. At first glance, this study seems to support the idea that a person's capacity to detect external stimuli is more attenuated during phasic REM sleep than during tonic REM sleep. However, it is not clear that this is the case because behavioural responsiveness may be an invalid measure of the perception of external stimuli during sleep. Burton *et al.* (1988) found that a tone was incorporated into a dream even when no instructed behavioural response occurred. This finding suggests that the absence of an instructed behavioural response to a stimulus during sleep does not necessarily mean that the stimulus remains undetected. This assumption is in agreement with Price and Kremen's (1980) idea that subjects may perceive presented stimuli equally well during tonic and phasic REM sleep and the increased threshold for behavioural response during phasic REM sleep may be as a result of possible muscle atonia.

One way to clarify the question of possible differences in the processing of external stimuli between phasic and tonic REM sleep is to use the event-related brain potential (ERP) method. It provides a direct measure of stimulus-elicited electric changes in brain function. Early studies in which ERPs were measured

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**Table 1** ERPs to the standard (std), small deviant (small dev), and large deviant (large dev) tones within the 50 ms time windows of the waking P3 and REM-P3 waves during which reliable differences were found among phasic REM sleep, tonic REM sleep, and wakefulness. The shown values are the mean μV values of the various time windows. Standard deviations are reported in parentheses.

| | *350–400 ms* | | | *400–450 ms* | | | *450–500 ms* | | | *500–550 ms* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Phasis REM* | *Tonic REM* | *Awake* | *Phasic REM* | *Tonic REM* | *Awake* | *Phasic REM* | *Tonic REM* | *Awake* | *Phasic REM* | *Tonic REM* | *Awake* |
| Std | | | | | | | | | | | | |
| Fz | −0.59 | −0.29 | −0.37 | −0.61 | −0.11 | −0.66 | −0.82 | −0.46 | −0.54 | −1.30 | −0.45 | −0.77 |
| | (2.92) | (1.95) | (1.03) | (3.02) | (1.48) | (1.08) | (3.57) | (1.79) | (1.44) | (4.16) | (1.60) | (1.45) |
| Cz | 0.07 | 0.04 | −0.49 | 0.22 | −0.09 | −0.73 | −0.49 | −0.57 | −0.57 | −1.13 | −0.47 | −0.72 |
| | (2.25) | (1.87) | (0.78) | (2.32) | (2.00) | (0.77) | (2.82) | (1.91) | (0.97) | (3.52) | (2.36) | (0.84) |
| Pz | −0.44 | −0.08 | −0.49 | 0.07 | −0.18 | −0.70 | −0.51 | −0.65 | −0.65 | −1.14 | −0.41 | −0.80 |
| | (2.65) | (1.96) | (0.78) | (2.53) | (1.51) | (0.74) | (2.79) | (1.68) | (0.88) | (3.29) | (1.75) | (0.84) |
| Small dev | | | | | | | | | | | | |
| Fz | −0.28 | −1.76 | −0.09 | −0.10 | −1.33 | −0.45 | −1.11 | −0.43 | −1.07 | −0.95 | −0.32 | −1.10 |
| | (4.16) | (3.09) | (2.58) | (4.10) | (2.61) | (2.26) | (3.71) | (2.97) | (2.20) | (3.18) | (2.61) | (2.15) |
| Cz | 0.52 | −1.54 | 0.19 | 0.74 | −1.38 | −0.62 | −0.54 | −0.75 | −0.72 | −0.69 | −0.65 | −0.29 |
| | (4.35) | (2.87) | (1.42) | (4.38) | (2.91) | (1.64) | (4.24) | (2.87) | (1.94) | (3.70) | (2.57) | (1.51) |
| Pz | 1.43 | −0.48 | 1.33 | 1.97 | −0.59 | 0.38 | 0.95 | −0.39 | 0.22 | 0.14 | −0.84 | 0.70 |
| | (4.44) | (2.73) | (1.36) | (5.17) | (2.52) | (1.85) | (4.92) | (2.75) | (1.83) | (4.58) | (3.34) | (1.56) |
| Large dev | | | | | | | | | | | | |
| Fz | −1.41 | −1.32 | 3.67 | −1.80 | −0.34 | 0.60 | −1.51 | 0.20 | −1.63 | −0.46 | 0.87 | −1.84 |
| | (4.92) | (4.06) | (3.60) | (4.79) | (4.15) | (1.88) | (4.84) | (4.15) | (2.30) | (4.55) | (4.44) | (2.23) |
| Cz | −0.21 | 1.09 | 4.47 | −1.03 | 3.01 | 1.88 | −1.14 | 3.98 | 0.36 | −0.66 | 4.18 | 0.23 |
| | (2.93) | (4.23) | (4.68) | (4.01) | (5.69) | (3.62) | (4.01) | (4.83) | (3.13) | (3.60) | (5.09) | (2.80) |
| Pz | 2.56 | 5.22 | 6.39 | 1.69 | 6.41 | 4.38 | 0.48 | 6.26 | 2.66 | −0.53 | 4.52 | 2.09 |
| | (3.48) | (5.29) | (4.94) | (4.41) | (7.24) | (4.19) | (4.32) | (6.84) | (3.44) | (4.01) | (6.51) | (2.99) |

to one type of stimulus showed that ERPs were flat during REM sleep when compared with ERPs of NREM sleep (Williams *et al.* 1962; Weitzman and Kremen 1965). This finding led to the assumption that the capacity for stimulus processing may be very limited during REM sleep. However, more recent ERP studies have revealed that the brain's capacity for stimulus processing may not be so limited during REM sleep as previously thought. These studies have used so-called 'oddball' paradigm in which ERPs are measured to repetitive standard and rare deviant stimuli. Bastuji *et al.* (1995) found that a deviant tone, but not a standard tone, elicited a parietally distributed positive wave (called REM-P3 hereafter) that resembled a waking P3 deflection. The P3 deflection is usually considered to be an indication of complex stimulus processing reflecting stimulus evaluation and the revision of the cognitive model of the environment (Donchin and Coles 1988). The amplitude of REM-P3 was markedly lower and its latency was longer when compared with the waking P3 wave. In fact, a REM-P3 could be detected in only 73% of the 6-min recording sessions. However, all the subjects showed a REM-P3 at least once. The authors assumed that the inconsistency of the REM-P3 may be as a result of differences in stimulus processing during the phasic and tonic periods. The study of Van Sweden *et al.* (1994) also showed a REM-P3 to a deviant tone.

The objective of this study was to examine stimulus processing during phasic and tonic periods of REM sleep with the ERP method. The purpose was to compare electric brain responses to frequent standard tones and infrequent deviant tones between phasic and tonic REM sleep. The focus was on ERPs to the deviant tones. In wakefulness, these stimuli are know to elicit two responses of interest, namely the P3 (see above) and mismatch negativity (MMN). The MMN has been claimed represent an automatic, attention-independent response to a stimulus deviation and its function is probably to initiate an attentional switch to a change in an unattended auditory input (Näätänen 1990, 1992). In addition to the comparisons between tonic and phasic REM sleep, the processing of auditory stimuli between REM sleep and the waking state was compared.

## METHODS

### Subjects

Fifteen healthy young volunteers (eight women and seven men, aged 19–35 y) served as the subjects. Before the beginning of the experiment, the subjects were informed about the purpose and course of the experiment and were told that they could cancel their participation at any point. Two of the subjects had an insufficient number (<20) of ERP responses during either the phasic or tonic periods of REM sleep. These subjects were excluded from the analysis.

### Procedure and stimuli

The subjects slept two nights in an electrically and acoustically shielded sleep chamber in the laboratory. The use of alcohol

and drugs was forbidden for 24 h prior to the experimental night. The data reported in this study were collected during the first night in the laboratory for seven subjects and during the second night in the laboratory for eight subjects. The subjects read a self-selected book either in the evening prior to starting to sleep or in the morning after sleeping all night in the laboratory. During the reading session, the ERPs were recorded as in sleep. The subjects were told that they would be presented tones while reading and sleeping but that they did not have to attend or respond to these stimuli.

An AMIGA 2000 computer was used to produce the stimuli which were delivered by a loudspeaker positioned behind the lying subject's head. The stimulus stream consisted of a frequent standard stimulus ($P=97\%$) of 1000 Hz and an infrequent small and large deviant tone ($P=1.5\%$ for each) with pitches of 1100 and 2000 Hz, respectively. The constant inter-stimulus interval (ISI) was 625 ms and the interval between two consecutive changes in the homogeneous stimulus stream varied randomly between 20 and 40s All the tones were presented with an intensity of 50 dB, and they had an rise/fall time of 10 ms and a duration of 50 ms.

### Recordings

EEG was recorded at Fz, Cz, and Pz referenced to the nose with silver-silver chloride electrodes using a 1 s time constant and a 100 Hz filter setting. Impedances were kept below 5 kΩ The saving period for the EEG data was 1500 ms before and 1500 ms after the onset of the pitch changes, and the sampling rate was 200 Hz. The data were saved on a hard disk for off-line computer analysis. Separate data were collected for off-line visual sleep stage scoring. They contained EEG, EOG and EMG epochs digitized at the 100, 50, and 200 Hz sampling rates, respectively. In this case, the saving period was 20 s and either the small or large pitch change was in the middle of the epoch. The electrode placement and sleep stage scoring were carried out according to the criteria of Rechtschaffen and Kales (1968).

### Data analysis

Prior to the analyses, all the trials containing an eye movement exceeding $+-75\,\mu V$ within the $-675$–$625$ ms time window were omitted. All the trials were also checked visually to exclude those containing motor artefacts.

ERPs were calculated for each subject and separately for the different conditions (reading session, phasic REM sleep and tonic REM sleep) and stimuli (standard, small deviant, large deviant). Each ERP trial contained four standard stimuli: two standards before and two standards after the deviant tone. ERPs were averaged for the standard stimulus that immediately preceded the deviant tone. Baseline-corrected ERP scores were calculated for P1 (50–100 ms), N1 (100–150 ms), mismatch negativity (MMN) (100–200 ms), P210 (150–300 ms), waking P3 (250–600), REM-P3 (350–600 ms) and late negativity (LN) (350–600 ms) waves. The response windows mentioned in parentheses were divided into 50 ms slices, and the mean value of each slice was used as a score. Scores for the MMN were obtained from the deviant minus standard difference waves.

Classification of the single ERP trials into phasic and tonic REM sleep was based on the occurrence of REMs. A trial was classified as tonic REM sleep when there was no REM 10 s prior to and 5 s after the pitch change. In the case of phasic state, there was at least one REM 0–5 s prior to the pitch change. In the other cases, a trial was excluded from the analysis.

All the 20 s epochs during which the subjects woke up were excluded. The accepted trials contained some minor movement arousals before and after the deviant tones but their likelihood was very low during both phasic (before: 1.1%, after: 4.3%) and tonic REM sleep (before: 1.4%, after: 3.6%).

### Statistical analysis

The occurrence of the waves was first tested by a MANOVA in which scores from all the channels were treated as concomitant dependent variables. When this showed a significant result ($P<0.05$) a channel-by-channel ANOVA was carried out to test at which channels the wave in focus differed significantly from zero. In the results section, only ANOVA results have been mentioned but this has usually been done only when the MANOVA reached significance. If an ANOVA result has been reported in the case of a non significant MANOVA result, it has been mentioned separately.

The differences among ERPs during tonic and phasic REM sleep and wakefulness were tested with a three-way ANOVA with repeated measures on State (wakefulness, phasic REM, tonic REM), Stimulus (standard, small deviant, large deviant), and Channel (Fz, Cz, Pz). The reported significance results were corrected with a Greenhouse–Geisser correction where appropriate.

## RESULTS

### ERPs during phasic REM sleep

*Standard tone*

The ERPs to the standard tone showed a P1 wave that was followed by early and late, long-lasting negative waves (Fig. 1). However, none of these waves reached significance.

*Small deviant tone*

The ERPs to the small deviant tone was similar to the ERPs to the standard tone except that a small P210 and REM-P3 wave could be observed (Fig. 1). Again the deflections failed to reach significance.

*Large deviant tone*

The ERPs to the large deviant tone revealed the same waves as the ERPs to the small deviant tone (Fig. 1). The P210 deflection reached significance at Fz ($F(1,12)=10.68$, $P<0.01$)

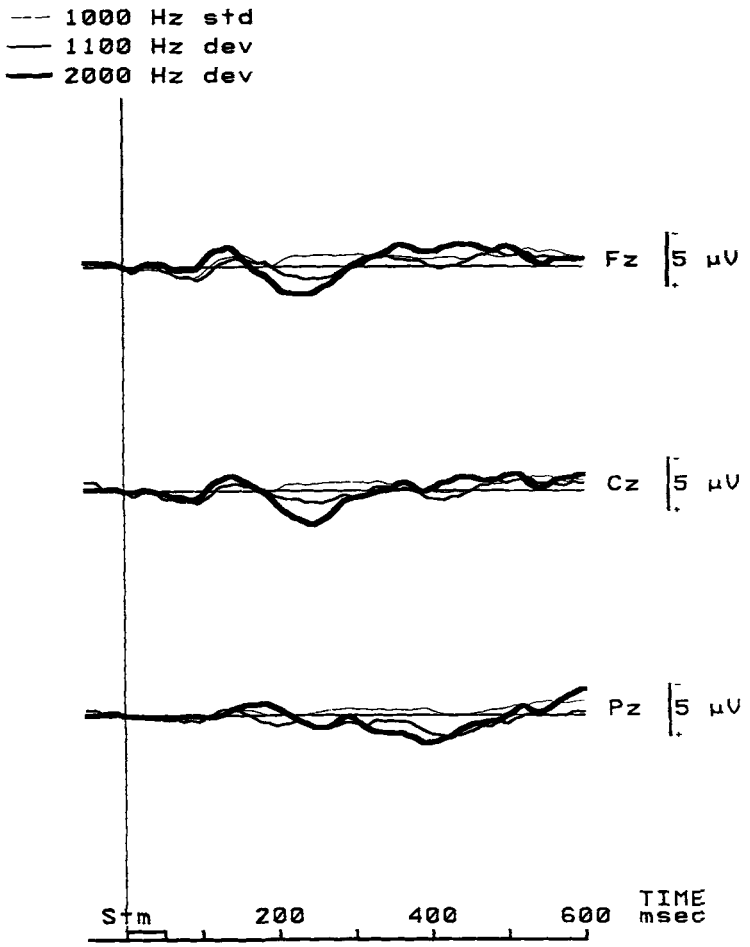


**Figure 1.** Grand average ERPs ($n=13$) to the standard tone (thin line, 993 trials), small deviant tone (second thickest line, 458 trials), and large deviant tone (thickest line, 475 trials) during *phasic* REM sleep.

and Cz *($F(1,12)=15.58$, $P<0.01$)* within the time window of 200–250 ms. The P3 approached the significance in the MANOVA analysis *($F(3,10)=3.47$, $P=0.059$)* within the time window of 350–400 ms. A channel-by-channel ANOVA showed that it was significant at Pz *($F(1,12)=7.08$, $P<0.05$)* where it could be expected to be the most pronounced.

## ERPs during tonic REM sleep

### *Standard tone*

The ERPs to the standard tone showed a P1 and P210 wave (Fig. 2). There was also a tendency towards a negativity between these waves. The P210 deflection was non significant but the P1 deflection reached significance at Fz ($F(1,12=15.84$, $P<0.01$) and Cz *($F(1,12)=5.02$, $P<0.05$)*.

### *Small deviant tone*

The ERPs to the small deviant tone revealed a frontally distributed P1 wave that was followed by a frontally distributed tendency for a negative wave, a P210 wave and late negativity (Fig. 2). Only the P210 wave reached significance (Fz: *$F(1,12)=5.87$, $P<0.05$)*.

### *Large deviant tone*

The ERPs to the large deviant tone contained the same waves as the ERPs to the small deviant tone except that the late negativity was almost invisible and a parietally distributed REM-P3 occurred within its latency range (Fig. 2). The P1 wave was the only wave that failed to reach significance. The P210 was significant for all the channels within the latency range of 200–300 ms (Fz: *$F(1,12)=8.26$–$28.68$, $P<0.05$–$0.001$*, Cz: *$F(1,12)=14.13$–$19.71$, $P<0.01$*, Pz: *$F(1,12)=7.18$–$13.62$, $P<0.05$*). In the case of REM-P3, the significance was reached at Pz within the latency range of 350–450 ms *($F(1,12)=10.19$–$12.67$, $P<0.01$)*. The REM-P3 was significant within the latency range of 450–550 ms at Cz *($F(1,12)=8.78$–$8.83$, $P<0.05$)* and Pz *($F(1,12)=6.27$–$10.88$, $P<0.05$–$.01$)*.

## ERPs during wakefulness

### *Standard tone*

The ERPs to the standard tone was characterized by a long-lasting negative wave within the latency range of 100–400 ms and it was followed by another negative wave (Fig. 3). These waves could not be separated from each other at Pz. The earlier

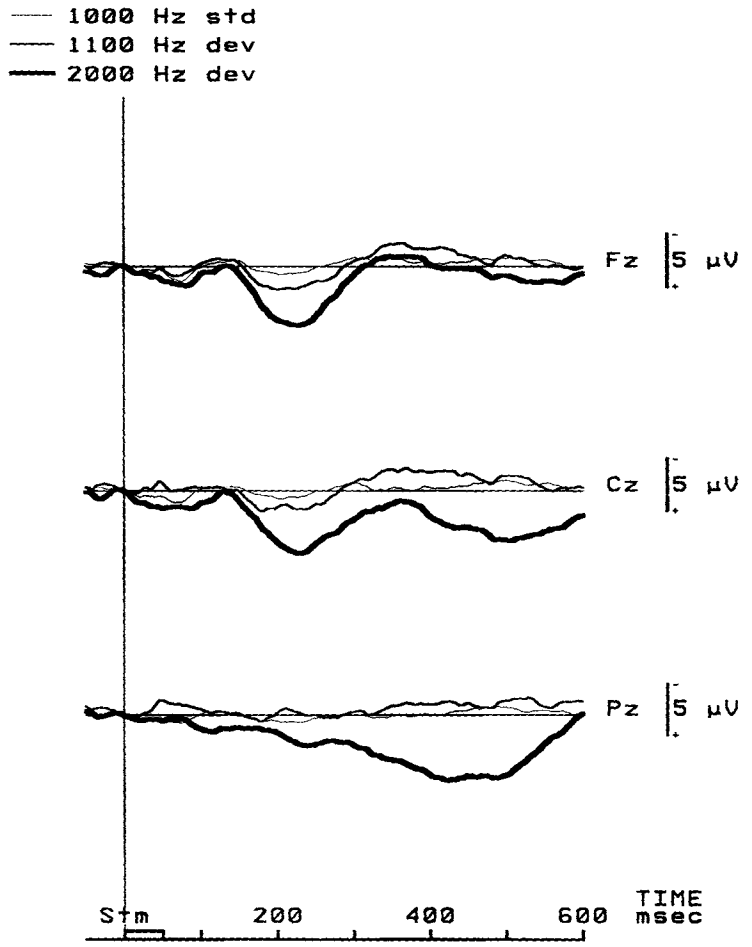


**Figure 2.** Grand average ERPs ($n=13$) to the standard tone (thin line, 1037 trials), small deviant tone (second thickest line, 516 trials), and large deviant tone (thickest line, 521 trials) during *tonic* REM sleep.

negativity reached significance for all the channels within the latency range of 250–350 ms (Fz: *F(1,12)=5.31–7.56, P<0.05*, Cz: *F(1,12)=12.93–21.31, P<0.01*, Pz: *>F(1,12)=8.34–10.86, P<0.05–0.01*). The later negative wave was significant at Cz within the time window of 500–550 ms *(F(1,12)=9.51, P<0.01)* and at Pz within the latency range of 450–550 ms *(F(1,12)=7.09–11.65, P<0.05–0.01)*.

*Small deviant tone*

The ERPs to the small deviant tone consisted of a small non significant P1 wave that was followed by a mismatch negativity (MMN), small, parietally distributed P3 deflection, and a non significant, frontally distributed late negative wave (Fig. 3). The MMN reached significance within the time window of 150–200 ms at Fz *(F(1,12)=15.75, P<0.01)* and at Cz *(F(1, 12)=11.78, P<0.01)*. The same held true for the P3 wave at Pz within the time slice of 350–400 ms *(F(1,12)=12.43, P<0.01)*.

*Large deviant tone*

The ERPs to the large deviant tone contained the same waves as in the case of the small deviant tone (Fig. 3). Only the P1 wave failed to reach significance. A reliable MMN occurred at all the channels within both time slices of the MMN (Fz: *F(1,12)=20.08–18.53, P<0.01*, Cz: *F(1,12)=20.61–10.82, P<0.01)*, Pz: *F(1,12)=5.91–4.73, P<0.05*). The P3 reached significance at Fz within the time slice of 350–400 ms *(F(1, 12)=13.52, P<0.01)*, at Cz within the latency range of 250–400 ms *(F(1,12)=6.65–11.86, P<0.05–0.01)*, and at Pz within the latency range of 250–550 ms *(F(1,12)=6.37–22.19, P<0.05–0.01)*. A reliable late negative wave could be detected at Fz within the latency range of 400–500 ms *(F(1,12)= 6.58–8.88, P<0.05)*.

**ERP differences among phasic REM, tonic REM, and wakefulness**

*P1 wave*

The State (awake, tonic REM, phasic REM) *Stimulus (standard, small deviant, large deviant) *Channel (Fz, Cz, Pz) ANOVA for repeated measures showed that the amplitude of the P1 wave differed significantly among the states *(F(2,24)= 4.38, P<0.05, ε=0.85442)*. None of the interactions including the State factor reached significance. When the states were compared pairwise it was found that the P1 amplitude was

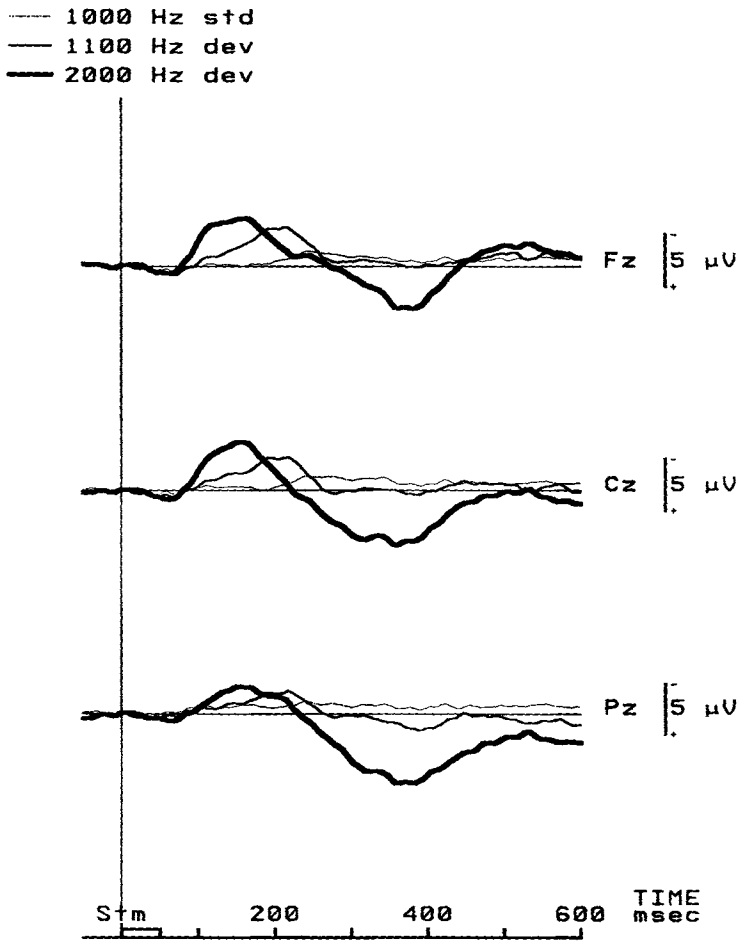


**Figure 3.** Grand average ERPs ($n=13$) subjects to the standard tone (thin line, 2631 trials), small deviant tone (second thickest line, 1374 trials), and large deviant tone (thickest line, 1257 trials) during the reading session.

higher in tonic *($F(1,12)=5.96$, $P<0.05$)* and phasic REM sleep *($F(1,12)=5.23$, $P<0.05$)* than in wakefulness. However, these differences were as a result of the occurrence of the MMN in wakefulness. Its onset latency was at about 75 ms and thus it affected the P1 scores that were the mean values calculated from the time window of 50–100 ms. When the peak values were used, no reliable differences could be found between wakefulness and REM sleep. The substages of REM sleep did not differ significantly.

*MMN*

The three-way ANOVA showed that the ERPs differed among the states within the time windows of the MMN *($F(2,24)=5.20$–$8.74$, $P<0.01$–$0.05$, $\varepsilon=0.65543$–$0.79242$)*. The State *Channel interaction also reached significance within the time window of 150–200 ms *($F(4,48)=4.31$, $P<0.05$, $\varepsilon=0.56203$)*. Further comparisons showed that only the tonic REM sleep vs. wakefulness contrast reached significance within the latency of 100–150 ms. The difference waves were more negative during wakefulness than during tonic REM sleep *($F(1,12)=34.41$, $P<0.001$)*. Within the time window of 150–200 ms, the difference wave was more negative during wakefulness than during tonic REM sleep at all the channels (Fz: *$F(1.12)=24.46$, $P<0.001$*, Cz: *$F(1,12)=39.72$, $P<0.001$*, Pz: *$F(1,12)=7.25$, $P<0.05$*). The difference curve of wakefulness was also more negative than that of phasic REM sleep at Fz *($F(1,12)=10.49$, $P<0.01$)* and Cz *($F(1,12)=11.12$, $P<0.01$)*. Tonic and phasic REM sleep did not differ significantly.

*P210 wave*

The three-way ANOVA revealed that the amplitude of the P210 differed among the states within the latency of 150–250 ms *($F(2,24)=17.75$–$30.95$, $P<0.001$, $\varepsilon=0.86007$–$0.93928$)*. The State *Stimulus *Channel interaction also reached significance within the time window of 150–200 ms *($F(8,96)=3.36$, $P<0.05$, $\varepsilon=0.39574$)* and the State *Channel interaction within the 200–250 ms time window *($F(4,48)=6.67$, $P<0.01$, $\varepsilon=0.49504$)*.

Further comparisons within the latency of 150–200 ms revealed that the ERP to the small deviant tone was more positive during tonic REM sleep than during phasic REM sleep at Fz *($F(1.12)=5.03$, $P<0.05$)* and wakefulness at all

the channels (Fz: $F(1,12)=23.55$, $P<0.001$, Cz: $F(1,12)=23.35$, $P<0.001$, Pz: $F(1.12)=7.31$, $P<0.05$). The ERP of phasic REM sleep was also more positive than that of wakefulness at all the channels (Fz: $F(1,12)=14.11$, $P<0.01$, Cz: $F(1,12)=10.25$, $P<0.01$, Pz: $F(1,12)=7.02$, $P<0.05$). When the ERPs to the large deviant tone during tonic and phasic REM sleep were compared separately for each channel no reliable differences were found. However, these ERPs of REM sleep were more positive than those of wakefulness. In the case of tonic REM sleep, this was detected at all the channels (Fz: $F(1,12)=21.88$, $P<0.001$, Cz: $F(1,12)=19.63$, $P<0.001$, Pz: $F(1,12)=8.77$, $P<0.05$) and in the case of phasic REM sleep at Fz ($F(1,12)=36.30$, $P<0.001$) and Cz ($F(1.12)=14.36$, $P<0.01$).

Further tests within the latency of 200–250 ms showed that the ERPs were more positive during tonic REM sleep than during phasic REM sleep at Fz ($F(1.12)=16.42$, $P<0.01$) and Cz ($F(1,12)=8.75$, $P<0.05$) and wakefulness at all the channels (Fz: $F(1,12)=63.32$, $P<0.001$, Cz: $F(1,12)=52.64$, $P<0.001$, Pz: $F(1,12)=11.10$, $P<0.01$). Also the ERPs of phasic REM sleep were more positive than those of wakefulness at all the channels (Fz: $F(1,12)=36.46$, $P<0.001$, Cz: $F(1,12)=30.35$, $P<0.01$, Pz: $F(1,12)=8.94$, $P<0.05$).

*P3 wave*

The three-way ANOVA revealed that the amplitude of the P3 wave differed among the states within the latency range of 350–400 ($F(2,24)=5.48$, $P<0.05$, $\varepsilon=0.71677$). The State *Stimulus interaction approached the level of significance ($P=0.068$). Additional analyses showed that the ERPs were more positive during wakefulness than during tonic ($F(1,12)=5.64$, $P<0.05$) and phasic REM sleep ($F(1,12)=10.92$, $P<0.01$). This State effect tended to be the most pronounced for the large deviant tone. No reliable difference was found between tonic and phasic REM sleep.

The State *Stimulus interaction reached significance within the time window of 400–450 ms ($F(4,48)=2.90$, $P<0.05$, $\varepsilon=0.74993$). An additional analysis showed that the ERPs to the large deviant tone were more positive during tonic than during phasic REM sleep ($F(1,12)=5.52$, $P<0.05$). The other contrasts failed to reach significance.

The State *Stimulus *Channel interaction reached significance within the latency range of 450–550 ms ($F(8,96)=3.23$–$3.36$, $P<0.05$, $\varepsilon=0.40496$–$0.43942$). Further analyses revealed that the ERP to the large deviant tone was more positive during tonic REM sleep than during phasic REM sleep at Cz ($F(1.12)=8.93$–$17.19$, $P<0.05$–$0.01$) and Pz ($F(1,12)=7.02$–$10.87$, $P<0.05$–$0.01$) and wakefulness at Cz ($F(1,12)=6.52$–$7.32$, $P<0.05$). The contrasts between phasic REM sleep and wakefulness failed to reach significance.

When the time windows in which the waking P3 and tonic REM-P3 reached their maximum amplitudes were compared no reliable difference could be found between the amplitudes of the deflections. However, the peak latency of the waking P3 (369 ms, SD = 64.0) was significantly shorter than that of the tonic REM-P3 (439 ms, SD = 54.5) ($F(1,12)=5.59$, $P<0.05$).

## DISCUSSION

The present study showed that the phasic and tonic periods of REM sleep differ in terms of the processing of auditory stimuli. This difference was seen for the P210 at Fz and Cz and the REM-P3 to the large deviant tone especially at Cz and Pz. Both waves were larger during tonic than during phasic REM sleep. No reliable MMN could be observed in REM sleep. The REM-P3 during the tonic state resembled the waking P3 except the peak latency of the REM-P3 was longer. However, prior to the latency of P3, these ERPs were dissimilar. A reliable MMN and P210 occurred only during wakefulness and sleep, respectively.

The present results are in agreement with the finding by Price and Kremen (1980) who showed an increased behavioural response threshold for external stimuli during phasic REM sleep. A central issue is the function of the REM-P3 in this context. One hypothesis is that it is a counterpart of the waking P3. There is some evidence supporting this idea. The topographies of waking and REM-P3 are very similar (Bastuji *et al.* 1995; the present study). Both responses occurred more clearly to the large stimulus change than to the small change. The present study also showed that the REM-P3 is smaller when the brain can be expected to be more preoccupied by ongoing mental activity. This is a consistent finding for the waking P3, which has been shown to be smaller for stimuli in a secondary task when a primary task has been made perceptually more difficult (Israel *et al.* 1980; Kramer *et al.* 1983). There is no empirical evidence supporting the hypothesis that the waking and REM-P3 reflect different neural processes. Our finding that the peak latency of REM-P3 during the tonic state was longer than that of P3 during the reading situation is consistent with the results of the study by Bastuji *et al.* (1995). It can be considered a sensible finding because cognitive functions are known to become slower as alertness decreases (Dinges and Kribbs 1991). The hypothesis that the waking and REM-P3 reflect different neural processes is based more on the suggestion that stimulus evaluation is too elaborate form of stimulus processing to occur during sleep. However, previous studies have shown that a sleeping subject can behaviourally respond to external stimuli during REM sleep without awakening (e.g. Williams *et al.* 1966; Burton *et al.* 1988) and external stimuli can be incorporated into dreams (Hoelscher *et al.* 1981; Burton *et al.* 1988). In this light, the occurrence of the P3 wave during REM sleep does not seem to be an inconsistent finding.

A question of importance is whether the found difference in the REM-P3 between phasic and tonic REM sleep periods could be as a result of something other than the difference in the attentional resources. One possibility could be that an external stimulus also elicits greater early responses during tonic than during phasic REM sleep. This early processing can be expected to be independent of our attentional resources. It was found that the P210 was greater during tonic than during

phasic REM sleep. Thus the deviant stimuli were processed differentially by the brain prior to the stage that can be considered to be dependent on our attentional resources. In addition, there is some evidence that the processing of an auditory input is attenuated to some extent prior its arrival in the brain during REMs because of twitches in the ear muscles (Baust *et al.* 1964; Pessah and Roffwarg 1972). Currently, the effect of the differences in the early stimulus processing between phasic and tonic REM sleep on the elicitation of the REM-P3 wave during these states remains open. However, it seems that the found difference in the REM-P3 wave between phasic and tonic REM sleep can not be exclusively attributed to the difference in the availability of the attentional resources. However, it is probable that differences between the phasic and tonic states in stimulus processing and mental state are closely connected, the temporarily attenuated sensitivity to external stimuli providing a better condition in which to immerse in dream content during phasic REM sleep.

Another explanation for the ERP differences observed between phasic and tonic REM sleep could be that tonic REM sleep during which no REMs occurred could not be completely distinguished from other states of alertness. Especially, tonic REM sleep is at times difficult to distinguish from NREM sleep stages 1 and 2. This scoring of REM sleep was based on the criteria of Rechtschaffen and Kales (1968) that were applied for 20 s data epochs collected around the deviant stimuli. These rules are arbitrary and they do not absolutely ensure the discrimination between REM sleep and NREM sleep stages 1 and 2 but they are widely used and quite exact. The rules can be considered to ensure that tonic REM sleep could be differentiated from NREM sleep in most of the cases. The facts that the EMG was at its lowest level and prominent slow eye movements, vertex waves, and movement arousals typical of stage 1 sleep were absent during the REM epochs quite reliably assure the discrimination between tonic REM sleep and stage 1 sleep. Second, the finding that the P210 was larger during tonic than during phasic REM sleep should not occur if tonic REM sleep could not be distinguished from stage 1 sleep in a reliable way (see Bastuji *et al.* 1995). The ERP data also suggest that tonic REM sleep could be differentiated from stage 2 sleep. ERPs to distinctive stimuli are known to contain a N350, N550, P900 wave during stage 2 sleep but the present ERPs of REM sleep showed no signs of these waves. In addition, the REM epochs of 20 s showed no EEG events typical of stage 2 sleep (K-complexes, sleep spindles) which also support the view that these epochs did not represent stage 2 sleep.

These data show that the same stimuli produce both similar and dissimilar brain responses during the waking state and phasic and tonic REM sleep. As has already been mentioned, the occurrence of late, parietally distributed positive wave to the large stimulus deviation was very similar during the reading session and REM sleep. The shorter latency waves were rather different. The MMN seemed to occur only in the reading session and the P210 wave only during phasic and tonic REM sleep. The disappearance of a reliable MMN during REM sleep is consistent with the results of previous studies on the MMN during sleep (Paavilainen *et al.* 1987; Nielsen-Bolhman *et al.* 1991; Sallinen *et al.* 1994; Winter *et al.* 1995). However, Campbell *et al.* (1992) and Loewy *et al.* (1996) reported on an MMN-like response during REM sleep. We observed a tendency for a negative wave within the MMN latency range especially during phasic REM sleep, but the same held true for the standard tone. It is possible that the tendency for an MMN was attenuated by the following P210 wave that possibly overlapped the negative deflection to the deviant tones during REM sleep.

## CONCLUSIONS

These results support the hypothesis that REM sleep can not be considered a homogeneous state in terms of the processing of external stimuli. In this sense, it is similar to NREM sleep that is known to be composed of various microstates, as indicated by various responses to an invariable stimulus (Ujszàszi and Halász 1986). The brain seems to be more sensitive to changes in an auditory input during tonic REM sleep than during phasic REM sleep. The late positive wave to a large stimulus deviation during tonic REM sleep closely resembles the waking P3 response. On the other hand, the absence of a reliable MMN suggests that the automatic, attention-independent processing of a stimulus change seems to be attenuated during tonic REM sleep. It is likely that this difference in stimulus processing between phasic and tonic REM sleep is closely connected to the difference in the orientation to dreams.

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