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Research report

Daytime vigilance in chronotypes: Diurnal variations and effects of behavioral sleep fragmentation

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Abstract

Vigilance levels of 12 morning types (M-types) and 12 evening types (E-types) were investigated after a baseline night, 2 nights of sleep fragmentation (5 min of forced awakening every half-hour) and a recovery night. Sleep timing was adjusted to the preferred sleep schedule of each subject. Daytime vigilance levels were assessed with test series including a scale of subjective alertness, a psychomotor vigilance task (PVT), a waking EEG recording, and a sleep latency test. Test series were administered every 4 h, beginning 1.5 h after wake time. On the baseline day, significant diurnal variations were found for each vigilance measure, except for the PVT. Diurnal variations were similar in M-types and E-types. Sleep fragmentation decreased vigilance levels on each measure, except the PVT. Effects of sleep fragmentation and recovery were similar in the two chronotypes. These results highlight the similarities in diurnal variations of vigilance in the two chronotypes when studied at their preferred sleep schedule. Results were also compared between chronotypes with extremely early or late circadian phases ("Extreme" subgroup) and between those with similar, intermediate circadian phases ("Intermediate" subgroup). Diurnal variations of subjective alertness and sleep latencies differed between "Extreme" chronotypes but were identical between "Intermediate" chronotypes. There were no major differences in the response to sleep fragmentation in any subgroup. Since phase angles differed by the same amount between chronotypes within each subgroup, the results suggest that a difference in phase angle cannot be the only source of the differences observed in diurnal variations between "Extreme" chronotypes.

Keywords: Morningness–eveningness; Alertness; Circadian rhythms; Individual differences; Sleep–wake schedule; Circadian phase; Sleep regulation; Phase angle

1. Introduction

A major source of interindividual variability in human circadian rhythms resides in morningness–eveningness: some individuals prefer to go to bed early and to wake up early (morning-types; M-types) whereas others go to bed late and wake up late (evening-types; E-types). M-types and E-types usually differ by approximately 2 h in both their sleep timing and circadian phase [3,4,16,25,26,28,35]. Differences in the dynamics of homeostatic sleep pressure have also been reported [29,39]. Since circadian and homeostatic processes are involved not only in sleep regulation but also in the regulation of alertness, performance and neurobehavioral functions [1,11,33,40], it can be expected that M-types and E-types also differ in the regulation of their levels of vigilance.

Diurnal variations in alertness and performance levels have been assessed many times in chronotypes. However, M-types and E-types were always tested at the same clock time, thereby forcing M-types to follow a later sleep–wake schedule – and E-types to follow an earlier one – than what they would spontaneously choose. As expected in such conditions, results showed that M-types had high levels of vigilance in the morning and low levels later during the day when compared to E-types [10,22,24,34–36,41]. To determine whether morningness–eveningness *per se* is associated with differences in diurnal variations of vigilance levels, participants need to be studied according to their preferential sleep–wake schedule.

It is not clear whether vigilance levels of M-types and E-types differ in response to increased sleep pressure. One study

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compared M-types and E-types after a 4-h sleep restriction and found no difference between the two chronotypes for subjective sleepiness or for daytime sleep propensity [41]. A questionnaire study showed no difference in subjective daytime sleepiness between M-types and E-types even if E-types were reporting a greater sleep debt during working days, suggesting the possibility that E-types were less sensitive than M-types to increased sleep pressure [38]. Finally, one study found that alertness levels decreased more in M-types than in E-types after an extension of time awake due to delayed bedtime [5]. However, in this case many parameters were modified simultaneously, including duration of time awake and sleep, and circadian phase of the sleep episode. To compare the response of vigilance levels to increased sleep pressure between M-types and E-types, it is necessary to use a procedure that modifies sleep pressure without changing the normal relationship between the sleep episode and the internal circadian phase.

We recently studied M-type and E-type subjects before, during, and after an increase in sleep pressure produced by 2 nights of behavioral sleep fragmentation. All subjects were sleeping according to their preferred sleep schedule and this sleep schedule was kept constant for the duration of the research protocol. Sleep analyses revealed a difference between M-types and E-types in markers of homeostatic sleep regulation. Compared to E-types, M-types showed a faster decay rate of slow-wave activity (SWA; 1–5 Hz) in the frontal derivation of the baseline sleep EEG [29], and a larger increase in SWA between baseline and recovery sleep after sleep fragmentation [31]. It is therefore possible that vigilance levels also respond differently in M-types than in E-types to increased homeostatic pressure caused by sleep fragmentation.

Our previous analyses revealed the presence of two subgroups in our volunteers [28]. The first subgroup included M-types and E-types with extremely early or late circadian phases ("Extreme" subgroup), as estimated with the salivary dim light melatonin onset (DLMO). The other subgroup included M-types and E-types with overlapping intermediate circadian phases ("Intermediate" subgroup). M-types and E-types of this "Intermediate" subgroup had chronotype scores [23] in the morning (59–69) or evening (28–37) range, respectively, and showed significant differences in their habitual sleep schedule (for details, see ref. [28]). However, they had similar DLMOs. Differences in the dynamics of homeostatic sleep pressure were significant only between M-types and E-types of this "Intermediate" subgroup [30,32]. If daytime vigilance levels were related to the dynamics of homeostatic response to increased sleep pressure, differences in vigilance levels in response to sleep fragmentation should also be specific to the "Intermediate" subgroup. Another interesting feature of these subgroups was that they differed in the interval between the DLMO and the habitual wake time (the "phase angle"): in the extreme subgroup, the phase angle was about 1.6 h *longer* in M-types than in E-types, whereas in the intermediate subgroup, the phase angle was 1.8 h *shorter* in M-types than in E-types. Therefore, these subgroups represent an interesting model to explore the influence of different phase angles of circadian wake propensity on the diurnal variation of vigilance levels.

In this report, we first examine diurnal variations in various measures of daytime vigilance in M-type and E-type individuals assessed when sleeping according to their preferred sleep–wake schedule. In this condition, variations in vigilance levels were expected to reflect the spontaneous levels of wakefulness associated to morningness–eveningness without interference from sleep restriction or from an imposed sleep schedule. We then present daytime vigilance levels in the two chronotypes in response to increased homeostatic sleep pressure produced with behavioral sleep fragmentation, before and after a night of recovery. Finally, vigilance results are compared between M-types and E-types having an intermediate phase position ("Intermediate" subgroup), and between M-types and E-types with an extremely early or late circadian phase ("Extreme" subgroup).

2. Methods

2.1. Subjects

M-type and E-type participants (19–34 years) were recruited using a French version of the Morningness–Eveningness Questionnaire (MEQ; Horne and Östberg [23]). Twenty-four subjects completed the study: 12 M-types (MEQ scores 59–71, mean 65.9 ± 1.1) and 12 E-types (MEQ scores 27–40, mean 32.7 ± 1.2). There were 6 women and 6 men in each group. Age was similar in the two groups (M-types: 24.7 ± 1.5 years; E-types: 23.4 ± 0.7 years). All subjects were in good physical and psychological health, and had no sleep complaint. Enrolled subjects had a regular sleep schedule with a habitual sleep duration between 7 and 9 h. A 24-h laboratory screening confirmed the absence of sleep and vigilance disorder by polysomnography and a multiple sleep latency test (MSLT). Inclusion criteria were: sleep efficiency higher than 85%, night sleep latency shorter than 30 min, apneas/hypopneas index and periodic leg movements index lower than $5\ h^{-1}$, and mean diurnal sleep latency longer than 7 min. Subjects had no night work experience in the past year and no transmeridian travel in the past 3 months. They were all non-smokers and reported not using drugs or medications, except oral contraceptives. Women not using hormonal contraception (3 M-types and 4 E-types) were studied during the follicular phase of their menstrual cycle. Each subject signed an informed consent form approved by the hospital ethics committee and received a financial compensation.

2.2. Procedures

Sleep schedules were determined according to each subject's preferred bedtime and wake time, using information from screening sleep diaries during free days, and preferred wake time and bedtime as reported in the MEQ. The final decision for the study sleep schedule was made after discussion with the subject to ensure that it was close to the schedule that he/she would spontaneously adopt. Bedtime and wake time were determined for a sleep duration of 8 h, similar to the habitual sleep duration reported by the two groups of subjects (7.8 ± 0.2 h for M-types and 8.0 ± 0.2 h in E-types [28]). On average, self-selected sleep schedules were 2.6 h earlier in M-types (23:08 to 07:08 h $\pm$ 11 min) than in E-types (01:45 to 09:45 h $\pm$ 17 min). Subjects were requested to follow their selected sleep schedule ($\pm$30 min) for 7 days prior to laboratory admission. Compliance was verified by sleep diaries and by 24-h ambulatory measures of activity and light exposure (Actiwatch-L, Mini-Mitter Co., Bend, OR).

After the week of ambulatory monitoring, subjects were admitted to the laboratory for 5 consecutive days and nights. Circadian phase was assessed by the onset of melatonin secretion (DLMO) determined in saliva samples and by the estimated minimum of core body temperature (T_{min}) recorded during a normal 24-h sleep–wake cycle. On average, circadian phase was earlier in M-types than in E-types (melatonin onset: 20:41 $\pm$ 27 min vs. 23:23 $\pm$ 25 min and temperature minimum: 04:17 $\pm$ 23 min vs. 06:17 $\pm$ 29 min, respectively). The interval between wake time and circadian phase (the "phase angle") was similar in M-types and E-types (interval with DLMO: 10.60 ± 0.4 h vs. 10.66 ± 0.4 h;

interval with T_{min}: 3.00 ± 0.3 h vs. 3.78 ± 0.3 h, respectively). Detailed information on circadian phase assessments of these subjects is reported in a previous publication [28].

In the laboratory, the subjects slept according to their individual sleep schedule for 5 consecutive nights: an adaptation night, a baseline night (BL), 2 nights of behavioral sleep fragmentation (FR1 and FR2) and a recovery night (REC). During the nights of sleep fragmentation, subjects were awakened for 5 min every half-hour, for a total of 15 awakenings per night [18]. For each awakening, a technician knocked on the door and entered the room with a small flashlight. Subjects had to interact verbally with the technician for the entire 5 min. Room light was not turned on and subjects were not required to open their eyes. Another technician stayed in the control room to keep track of the time and to confirm wakefulness according to on-line EEG recordings. Compared to BL, sleep fragmentation increased time awake by about 2 h in FR1 and by about 1.3 h in FR2. Sleep architecture, including the increase of time awake during the nights of behavioral sleep fragmentation, was similar in M-types and E-types for BL, FR1, FR2 and REC nights (for details, see ref. [31]).

Daytime vigilance was assessed during the days following baseline, fragmentation and recovery nights (dBL, dFR1, dFR2 and dREC) using a series of 4 different tests. Test series were administered every 4 h: 1.5, 5.5, 9.5 and 13.5 h after wake time. The series scheduled 13.5 h after wake time were not administered on the last day (dREC). Including pauses between the tests, each series lasted a maximum of 65 min. The tests were administered in the following order: a 10-cm visual analog scale of alertness (VAS) [27] with the inscription "very sleepy" on the left end and the inscription "very alert" on the right end, a 10-min visual psychomotor vigilance task (PVT) [13], a 2- to 4-min waking EEG recording (wEEG) with eyes open fixing a black cross on the wall [2], and a sleep latency test of a maximum duration of 25 min (MSLT) [9].

2.3. Data analysis

For each VAS, alertness level was measured by the distance, in centimeters, between the left end of the scale and the line traced by the subject. For the PVT, the 10% slowest reaction times (RTs, transformed in 1/RT for statistical analyses) were used to assess neurobehavioral performance as it is the parameter most sensitive to the effects of increased sleep pressure [14,21]. The PVT data of one M-type woman were missing due to technical problems during dBL. For both wEEG and MSLT recordings, EEG, EOG and chin EMG electrodes were used in reference to linked-ears (10 kΩ resistance). Signals were amplified with a polygraph Grass Model 15A54 (Astro-Med Inc., West-Warwick, USA; gain 10000, bandpass 0.3–100 Hz) and digitized at a sampling rate of 256 Hz (Harmonie 5.1, Stellate Systems, Montreal, Canada). For wEEGs, spectral analysis was performed with a commercial software package (Sensa, Stellate Systems, Montreal, Canada) on EEG selections free of artifact. For each wEEG test, the number of seconds included in the analysis varied between 38 and 140 (mean and S.E.M. = 97.3 ± 1.6) in M-types, and between 8 and 208 (mean ± S.E.M. = 97.2 ± 2.3) in E-types. The Fz derivation was chosen for the analyses because the EEG recorded from the frontal derivations is known to be most sensitive to increased sleep pressure, in both sleep and wakefulness [8,19,29]. Spectral power was obtained by fast Fourier transforms (FFT) computed on 2-s sections using a Hanning window tapering resulting in a 0.5 Hz spectral resolution. For each wEEG recording, spectral power was averaged for the 5–9 Hz frequency band, as higher power in this frequency band is commonly associated with lower levels of alertness [2,7,15]. For the MSLT, sleep latencies were determined using the C3 derivation and defined as the time from lights off to the first minute of stage 1 or to the first epoch of any other sleep stage, or as 25 min if no sleep occurred.

2.4. Statistical analysis

Each measure was transformed in percent of the individual's mean of the four results obtained during dBL. To compare diurnal variations between M-types and E-types at baseline, Group-by-Hour (2 × 4) analyses of variance (ANOVAs) were used to assess the interaction between the 2 groups and the 4 tests sessions of dBL. To compare the effects of sleep fragmentation, Group-by-Day-by-Hour (2 × 3 × 4) ANOVAs were computed to assess between-group differences in vigilance levels at the 4 testing times during dBL, dFR1 and dFR2. For this set of analyses, wEEGs data of one E-type man were missing. Finally, Group-by-Day-by-Hour (2 × 2 × 3) ANOVAs were used to compare between-group differences in the changes in vigilance levels between baseline and recovery, for the first 3 testing times of dBL and dREC. The same set of analyses was repeated for the subgroup of subjects with intermediate phases (6 M-types with DLMO between 21:07 and 23:03 h, aged 25.0 ± 1.2 years, and 6 E-types with DLMO between 21:18 and 23:04 h, aged 23.3 ± 2.2 years), and for the subgroup of subjects with extremely early (6 M-types, DLMO between 17:25 and 20:59 h, aged 26.2 ± 2.1 years) or late (6 E-types, DLMO between 23:57 and 01:35 h, aged 21.8 ± 0.3 years) circadian phases. Huynh/Feldt corrections were used for repeated measures but the original degrees of freedom are reported. Significant interactions were decomposed with simple effect analysis. Statistical significance was set to 0.05 and results are presented in mean ± S.E.M.

3. Results

3.1. All subjects

3.1.1. Diurnal variations during baseline

Significant diurnal variations were found for the VAS, wEEG and MSLT (Hour effects: $F_{3,66} \geq 3.7$, $p \leq 0.03$), but not for the PVT (see dBL in Fig. 1). There was no significant difference in diurnal variations between the two groups. A Group-by-Hour interaction approached significance for the VAS ($F_{3,66} = 2.7$, $p = 0.07$): lowest levels of subjective alertness in E-types were on the first test, 1.5 h after awakening, whereas they were lowest on the last test, 13.5 h after awakening, in M-types (Fig. 1).

3.1.2. Effects of sleep fragmentation

Sleep fragmentation produced similar Day effects in the two groups for VAS, MSLT and wEEG ($F_{2,42–2,44} \geq 4.8$, $p \leq 0.01$; see Fig. 1). On dFR1, compared to the 100% dBL mean value, subjective alertness on the VAS decreased (90.4 ± 3.1; $p < 0.01$), sleep latencies on the MSLT shortened (75.4 ± 5.3%; $p < 0.01$), and 5–9 Hz wEEG activity increased (132.5 ± 7.0%; $p < 0.01$). On dFR2, the only significant Day difference compared to dBL was the increase in 5–9 Hz wEEG activity (132.7 ± 5.4%; $p < 0.001$). There was no effect of sleep fragmentation on PVT 10% slowest RTs. There was no significant Group-by-Day or Group-by-Day-by-Hour interaction for any variable.

3.1.3. Recovery from sleep fragmentation

Comparisons between baseline (first 3 test series only) and recovery yielded different results depending on vigilance measures. VAS showed a Group-by-Day interaction ($F_{1,22} = 6.5$, $p < 0.05$) (Fig. 1). VAS results averaged on the first 3 tests of the day increased on dREC in E-types (109.1 ± 4.2% vs. 100.3 ± 1.9%; $p = 0.05$) but tended to decrease in M-types (98.9 ± 4.2% vs. 105.5 ± 1.9%; $p = 0.10$). A Day effect was found for the MSLT ($F_{1,22} = 12.9$, $p < 0.01$), with longer daytime sleep latencies for the average of the first 3 tests on dREC than on dBL (161.0 ± 21.9% vs. 82.0 ± 4.2%; Fig. 1). There was no significant effect on the PVT. For the wEEG, there was only a significant Hour effect ($F_{2,44} = 18.6$, $p < 0.01$; Fig. 1). There was no significant Group-by-Day-by-Hour interaction for any variable.

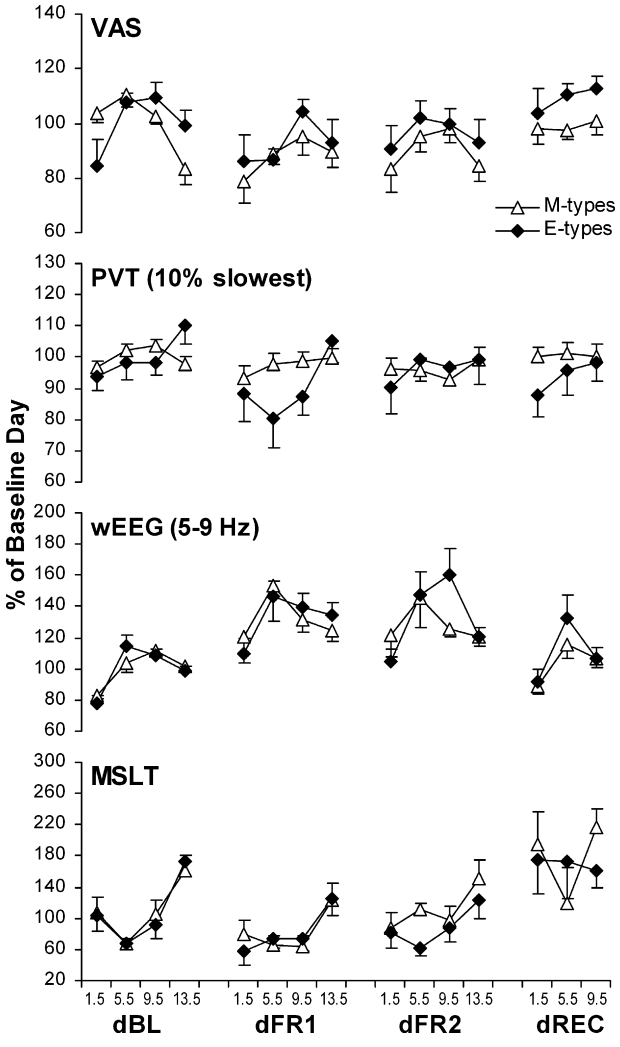

Fig. 1. Mean (and S.E.M.), expressed in percent of the baseline day mean, of the results of the 12 M-types (white triangles) and 12 E-types (black lozenges), for each vigilance test: subjective alertness (VAS), 10% slowest reaction times on the psychomotor task (PVT), spectral power in the 5–9 Hz frequency of the waking EEG (wEEG), and daytime sleep latencies (MSLT). Data are shown for each test series administered on the day following the baseline night (dBL), the first night of sleep fragmentation (dFR1), the second night of sleep fragmentation (dFR2), and the recovery night (dREC). For VAS, PVT and MSLT measures, higher values indicate higher levels of vigilance whereas for wEEG, higher values indicate lower levels of vigilance.

3.2. Subgroups of subjects

3.2.1. Diurnal variations during baseline

The trend for a Group-by-Hour interaction in VAS observed in the entire group of subjects was stronger when examined specifically within the subgroup with extreme circadian phases ($F_{3,30} = 3.2$, $p = 0.053$); the lowest levels of subjective alertness were on the first test in E-types (1.5 h after awakening) and on the last test in M-types (13.5 h after awakening). This is in clear contrast with the identical curves of diurnal variations observed in the subgroup of subjects with intermediate phases ($F_{3,30} = 0.2$, $p = 0.90$; see Fig. 2). In addition, a significant Group-by-Hour interaction was found for MSLT results only in the "Extreme" subgroup ($F_{3,30} = 3.3$, $p = 0.03$): E-types had longer sleep latencies on the last test (13.5 h after wake time) than on the first one (1.5 h after wake time) ($p < 0.01$), whereas M-types showed no difference between these 2 tests ($p = 0.8$). There was no significant interaction in any of the two subgroups for the PVT and the wEEG.

3.2.2. Effects of sleep fragmentation

Effects of sleep fragmentation were not significantly different between M-types and E-types in any of the two subgroups.

3.2.3. Recovery from sleep fragmentation

The comparisons between baseline and recovery showed a significant Group-by-Day interaction only in the "Extreme" subgroup for the VAS ($F_{1,10} = 6.9$, $p = 0.025$), with E-types having higher levels of subjective alertness during dREC than during dBL ($112.3 \pm 6.9\%$ vs. $97.8 \pm 3.1\%$; $p < 0.05$; Fig. 2) whereas similar levels were found in M-types ($98.1 \pm 6.9\%$ vs. $107.1 \pm 3.1\%$; $p = 0.2$). No other interactions were significant except a Group-by-Hour effect for the wEEG in the "Intermediate" subgroup ($F_{2,20} = 5.7$, $p = 0.01$), revealing an increased spectral power of the 5–9 Hz frequency band 5.5 h after awakening only in the E-types of this subgroup ($p < 0.01$ for both 1.5 h vs. 5.5 h and 5.5 h vs. 9.5 h after wake time; Fig. 2).

4. Discussion

4.1. Diurnal variations of vigilance levels in baseline

In this study, diurnal variations in vigilance levels of M-types and E-types were studied when wake times and bedtimes were individually adjusted to respect the spontaneous sleep schedule of the subjects. In this condition, there was no significant difference in diurnal variations of vigilance levels between the two groups, with only a trend for higher subjective alertness for the M-types in the morning and higher subjective alertness for the E-types in the evening. As indicated in the procedures, the averaged phase angle (interval between wake time and circadian phase) was the same in the two groups, which means that they were studied at the same internal phase. It was therefore expected that both M-types and E-types would show similar diurnal variations in vigilance levels within their episode of wakefulness.

Of great interest are the results obtained in the subgroups of "Extreme" and "Intermediate" chronotypes. Significant differences in diurnal variations were found only between M-types and E-types with extremely early (DLMO: 19:33 h ± 33 min) or late (DLMO: 24:36 h ± 16 min) circadian phases. In this subgroup, M-types reported higher subjective alertness (VAS) and showed longer daytime sleep latencies (MSLT) in the morning than E-types. The reverse was true in the evening. For the VAS, the diurnal pattern differed between the two chronotypes, showing a decrease in subjective alertness over the day in M-types and an increase in E-types (Fig. 2, left panel, VAS, dBL). For the MSLT, the typical "U" pattern was observed [37], but the shortest sleep latencies of the day were observed earlier in M-types (5.5 h after wake time) than in E-types (9.5 h after wake time) (Fig. 2, left panel, MSLT, dBL). Therefore, in subjects having early or late circadian phases, differences in diur-

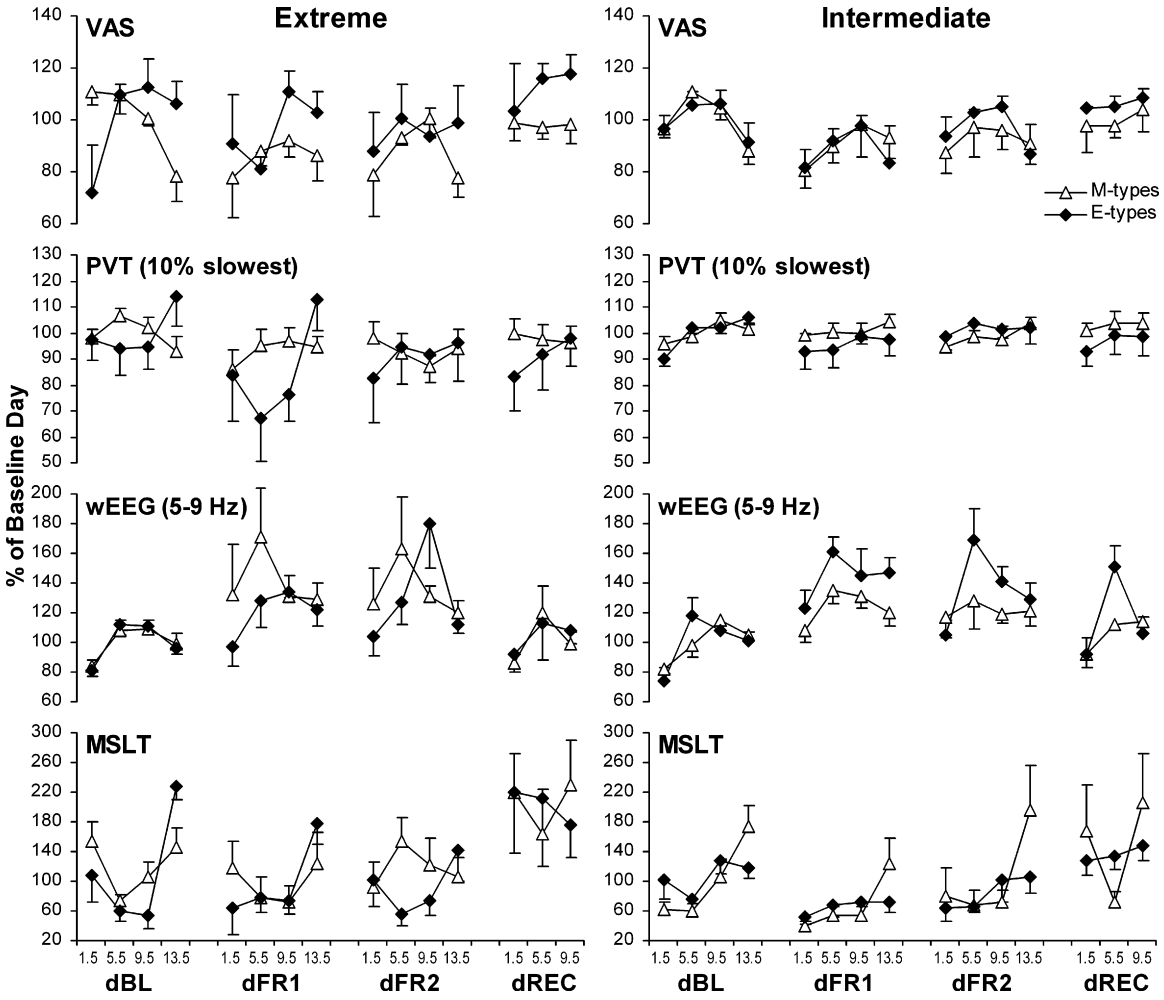

Fig. 2. Mean (and S.E.M.), expressed in percent of the baseline day mean, for each vigilance test: subjective alertness (VAS), 10% slowest reaction times on the psychomotor task (PVT), spectral power in the 5–9 Hz frequency of the waking EEG (wEEG), and daytime sleep latencies (MSLT). The left panel shows the results of the 6 M-types (white triangles) and the 6 E-types (black lozenges) with extremely early or late circadian phases ("Extreme" subgroup). The right panel shows the results of the 6 M-types (white triangles) and the 6 E-types (black lozenges) with intermediate circadian phases ("Intermediate" subgroup). Data are shown for each test series administered on the day following the baseline night (dBL), the first night of sleep fragmentation (dFR1), the second night of sleep fragmentation (dFR2), and the recovery night (dREC). For VAS, PVT and MSLT measures, higher values indicate higher levels of vigilance whereas for wEEG, higher values indicate lower levels of vigilance.

nal variations of subjective alertness and sleep propensity can be observed even when they follow their preferred sleep/wake schedule. As noted in other studies [3,16], M-types with an early circadian phase had a longer phase angle (DLMO–wake time = 11.63 ± 0.42 h) than E-types with a late circadian phase (DLMO–wake time = 9.98 ± 0.57 h; $p < 0.05$) [28], a difference probably due to variations in the length of the endogenous circadian period [17,20]. This phase angle difference means that on awakening, circadian wake propensity was already higher in M-types than in E-types, hence the higher levels of vigilance in the morning. Conversely, circadian wake propensity decreased earlier within the wake episode of M-types, producing lower levels of vigilance in the evening in M-types than in E-types.

In the subgroup of M-types and E-types with similar "Intermediate" circadian phases, the two chronotypes also showed a significant difference in phase angles, this time shorter in M-types (DLMO–wake time = 9.55 ± 0.25 h) than in E-types (DLMO–wake time = 11.37 ± 0.43 h; $p < 0.01$) [28]. In spite of this difference in phase angles, diurnal variations of vigilance levels were remarkably similar (Fig. 2, right panel, dBL). This unexpected observation shows that phase angles and diurnal variations in vigilance are not necessarily related, and suggests that the difference in phase angles observed in chronotypes of the "Extreme" subgroup is not the only reason for the differences found in their diurnal variations.

4.2. Response to sleep fragmentation

The procedure of behavioral sleep fragmentation induced a decrease in vigilance levels as assessed with subjective alertness (VAS), daytime sleep propensity (MSLT) and physiological arousal (wEEG). No significant effect was found on neurobehavioral functions measured with the PVT. The PVT was not sensitive to diurnal variations in vigilance levels and, similarly, it was not sensitive to the relatively small increase in sleep pressure caused by sleep fragmentation. This is consistent with the

results of previous studies on total sleep deprivation, where significant increases in RTs were observed only after more than 16 h of time awake [6,21].

The three measures sensitive to sleep fragmentation showed a similar decrease in vigilance levels in M-types and in E-types. This was true not only when the entire group of subjects was considered, but also when M-types and E-types were compared within the "Extreme" and "Intermediate" subgroups. It seems therefore that the difference previously described between chronotypes in the rate of decline of homeostatic sleep pressure [29,30] had no impact on vigilance levels following sleep fragmentation. Our analyses of the decline of slow-wave activity (1–5 Hz) during the nights of sleep fragmentation showed that the decline was faster in M-types than in E-types, but reached similar levels in both chronotypes upon awakening [31]. It remains possible that a more severe sleep restriction would favor subjects with a faster decrease of sleep pressure and produce a lower decrease in vigilance levels in M-types than in E-types. This prediction will have to be verified in future research.

4.3. Recovery from sleep fragmentation

The only significant effect of chronotype after the recovery night was for subjective alertness, E-types reporting higher levels during dREC than during dBL (Fig. 1). Analyses within the subgroups showed that this difference applied only to E-types of the "Extreme" subgroup, and was due essentially to higher subjective alertness 1.5 h after awakening on dREC compared to dBL (Fig. 2, left panel). This result could have been observed only by chance, considering the small number of subjects ($n = 6$) and the large individual variability in alertness at this time point. Besides, the significant increase in daytime sleep latencies observed in both groups of subjects on the last day of the protocol (Fig. 1) may reflect a general decrease in daytime sleep propensity due to the deepening of the preceding sleep episode (increased slow-wave sleep and slow-wave activity during the recovery night compared to the baseline night [31]). Furthermore, it is not excluded that the subjects' knowledge that they would be free to leave the laboratory at the end of that day, after 5 consecutive days of confinement, may have contributed to a general arousing effect.

Regarding the effects of sleep fragmentation, we expected to find a larger influence of chronotype in the "Intermediate" subgroup as it was specifically within this subgroup that significant differences were observed between M-types and E-types for the dynamics of homeostatic sleep pressure [30,32]. However, the only effect was a Group-by-Hour interaction for the wEEG, showing increased 5–9 Hz activity 5.5 h after awakening in E-types with intermediate phases (Fig. 2, right panel, wEEG, dBL and dREC). It is possible that this effect represents an enhancement of the normal diurnal variation in physiological arousal. Since circadian variations in vigilance levels are accentuated when homeostatic sleep pressure increases [11,12], a larger diurnal variation in E-types with intermediate phases may reflect a greater residual level of homeostatic pressure after the recovery night in this subgroup of subjects. However, this interpretation will remain speculative until future replication in a larger group of subjects.

In conclusion, our results suggest that differences in diurnal variations between M-types and E-types cannot be entirely explained by an imposed sleep–wake schedule or by a difference in the phase angle between circadian wake propensity and the sleep schedule. They suggest that another mechanism, probably associated with a difference in the endogenous period, can influence diurnal patterns of vigilance levels, mostly those related to subjective alertness and sleep propensity. The protocol of behavioral sleep fragmentation was able to decrease subjective alertness, increase daytime sleep propensity and increase EEG markers of sleepiness. These effects were very similar in M-types and in E-types, but differences could still be expected after a larger increase of sleep pressure, especially between M-types and E-types showing differences in homeostatic sleep regulation.

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