

Effects of Prior Light Exposure on Early Evening Performance, Subjective Sleepiness, and Hormonal Secretion

Mirjam Münch, Friedrich Linhart, and
Apiparn Borisuit
Swiss Federal Institute of Technology, Lausanne

Susanne M. Jaeggi
University of Michigan

Jean-Louis Scartezzini
Swiss Federal Institute of Technology, Lausanne

In sighted humans, light intensity, timing, exposure duration, and spectral composition of light are important to entrain the endogenous circadian pacemaker to the 24-h day-night cycle. We tested the impact of two realistic office lighting conditions during the afternoon on subjective sleepiness, hormonal secretion, and cognitive performance in the early evening hours. Twenty-nine young subjects came twice and spent 8 h (12:00–20:00) in our laboratory, where they were exposed for 6 h to either artificial light (AL) or to mainly daylight (DL). In the early evening, we assessed their salivary cortisol and melatonin secretion, subjective sleepiness, and cognitive performance (n-back test) under dim light conditions. Subjects felt significantly more alert at the beginning of the evening after the DL condition, and they became sleepier at the end of the evening after the AL condition. For cognitive performance we found a significant interaction between light conditions, mental load (2- or 3-back task) and the order of light administration. On their first evening, subjects performed with similar accuracy after both light conditions, but on their second evening, subjects performed significantly more accurately after the DL in both n-back versions and committed fewer false alarms in the 2-back task compared to the AL group. Lower sleepiness in the evening was significantly correlated with better cognitive performance ($p < .05$). In summary, even short-term lighting conditions during the afternoon had an impact on cognitive task performance in the evening. This rapid effect was only distinguishable on the second day of training, when a difficult task had been sufficiently practiced.

Keywords: n-back task, working memory, prior light effects, circadian, subjective sleepiness, daylight

Environmental lighting conditions enable the synchronization of the endogenous biological clock in the mammalian suprachiasmatic nuclei (SCN) to the solar 24-h day–night cycle (Aschoff, 1984). Hereby, light intensity, exposure duration, and spectral composition perceived via the eyes are crucial to reset the circadian phase in order to adapt to different day lengths. These phase shifts are best documented by circadian markers, such as pineal

melatonin secretion or the core body temperature rhythm (Czeisler et al., 1986). Light exposure during the evening and early night induces a phase delay, and light exposure in the early morning hours advances circadian phase the next day (Khalsa, Jewett, Cajochen, & Czeisler, 2003).

Beside these circadian effects of light, bright light exposure also has direct effects to suppress nocturnal melatonin secretion and acutely increase alertness, when compared to dim lighting conditions (Cajochen, Zeitzer, Czeisler, & Dijk, 2000; Phipps-Nelson, Redman, Dijk, & Rajaratnam, 2003; Rüter, Gordijn, Beersma, de Vries, & Daan, 2006; Zeitzer, Dijk, Kronauer, Brown, & Czeisler, 2000). A dose-dependent effect of light intensity has been shown for nighttime light exposures on alertness and melatonin suppression (Cajochen et al., 2000; Zeitzer et al., 2000). Daytime and nocturnal light exposures, acutely increased cognitive performance and sustained attention compared to dim lighting conditions (<7 lux), whether polychromatic white light or narrowband monochromatic light sources were used. (Badia, Myers, Boecker, Culpepper, & Harsh, 1991; Campbell & Dawson, 1990; Chellappa et al., 2011; Lockley et al., 2006). Higher executive functions and sustained attention were demonstrated to be more sensitive to brighter and to blue-enriched polychromatic light sources (Lockley et al., 2006; Vandewalle, Schmidt et al., 2007). Even relatively low illuminance levels in the evening, for example via blue computer screen

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Mirjam Münch, Friedrich Linhart, Apiparn Borisuit, and Jean-Louis Scartezzini, Solar Energy and Building Physics Laboratory, Swiss Federal Institute of Technology, Lausanne; Susanne M. Jaeggi, Department of Psychology, University of Michigan.

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Correspondence concerning this article should be addressed to Mirjam Münch, Solar Energy and Building Physics Laboratory, School of Architecture, Civil and Environmental Engineering, Ecole Polytechnique Fédérale de Lausanne, Station 18, CH-1015 Lausanne, Switzerland. E-mail: mirjam.munch@epfl.ch

background, could suppress melatonin and increase performance (Cajochen et al., 2011).

The above findings point to the important role of the spectral composition of the light flux. A third class of photoreceptors in the inner retina, the intrinsically photosensitive retinal ganglion cells (ipRGC), contain the photopigment melanopsin maximally sensitive in the blue range of visible light around 480 nm (Berson, Dunn, & Takao, 2002; Hattar, Liao, Takao, Berson, & Yau, 2002). The ipRGCs contribute to many biological effects, not only melatonin suppression and phase shifts, but also clock gene expression, the pupillary light reflex, alertness, thermoregulation, as well as brain activity, cognitive performance, and sleep (Brainard et al., 2001; Cajochen et al., 2006; Cajochen et al., 2005; Gamlin et al., 2007; Lockley, Brainard, & Czeisler, 2003; Lockley et al., 2006; Münch et al., 2006; Revell & Skene, 2007; Thapan, Arendt, & Skene, 2001).

Prior exposure to longer wavelengths of light increases the pupil response to blue light in humans (Mure et al., 2009). Prior exposure to different light intensities (including even dim room lighting conditions) have the potential to significantly influence the magnitude of melatonin suppression, the timing of melatonin secretion on the same evening and to shift its circadian phase the next day (Chang, Scheer, & Czeisler, 2011; Figueiro & Rea, 2010; Gooley et al., 2010; Hashimoto et al., 1997; Hébert, Martin, & Eastman, 2002; Smith, Schoen, & Czeisler, 2004). One applied study, performed with white-collar office workers over several weeks, revealed significantly greater subjective performance, alertness, and sleep quality under blue-enriched white light sources when compared to iso-illuminance white fluorescent tubes, indicating that lighting conditions at workplaces during work hours mediated subjective variables later in the day and beyond actual light exposure (Viola, James, Schlangen, & Dijk, 2008). Another study, where subjects were exposed to two different office lighting environments, reported higher subjective alertness in the early evening in response to brighter lighting conditions, as assessed from sleep logs (Gornicka, 2008).

Most people spend their days within buildings under different lighting environments, which range from daylight to artificial light only. At most workplaces, there is a mixed situation between the two principal light sources (Linhart, 2010). For the impact of light perception on nonvisual functions such as alertness, mood, and performance, those lighting conditions are likely to significantly contribute to modulation of alertness and productivity via the retinohypothalamic tract and melanopsin-dependent pathways. So far, (and as described above), only a few studies tested whether daytime lighting conditions have repercussions on alertness and cognitive performance in the (early) evening hours and none of them considered daylight as our most important and obvious source.

In the present study, we thus tested whether exposures to two different “realistic” office lighting conditions during the afternoon (including daylight) affect sleepiness, hormonal secretion, and cognitive performance in the early evening in healthy young subjects.

Method

Subject Screening

Healthy young subjects between 19 and 25 years were recruited via flyers at the Swiss Federal Institute of Technology Lausanne

(EPFL). Twenty-nine subjects (age: 23.6 ± 2.4 years; mean \pm SD; 12 women, 17 men) were included in the study. All subjects were free from medical or psychiatric disorders as assessed with a screening questionnaire and interview. Only healthy subjects not taking any medication and nonsmokers were included. Subjects reported normal sleep-wake cycles without any sleep disorders. None of them was an extreme morning or evening chronotype (mean 57.4 ± 7.2 ; mean \pm SD), as defined by the Horne-Östberg Questionnaire, except for one subject, who was a morning type. None had performed shift work or traveled across more than one time zone within 2 months prior to the study. The study protocol was approved by the local ethical review board and the procedures are in agreement with the Declaration of Helsinki. Before the study began, all subjects gave written informed consent.

Study Design

Subjects were asked to keep a regular sleep-wake cycle of approximately 8 hours, 7 days prior to the study beginning, with bed and wake times within self-selected target times of ± 30 min. Compliance was verified by a wrist activity monitor (Daqtix[®], Oetzen-Süttorf, Germany) as well as sleep logs. Subjects were requested to only moderately consume caffeine and alcohol and to completely abstain on study days. Subjects came to the laboratory on two subsequent days for 8 hours during the daytime and evening. The study started 4–5 hours after habitual wake time (mean habitual wake- and bedtimes were at $7:17 \pm 24$ min and $23:14 \pm 26$ min, respectively; mean \pm SD) and light exposure in the morning hours was not controlled.

During the first six hours of the study, subjects remained in a sitting position in an experimental testing room at our laboratory. They were allowed sedentary activities such as reading, writing, listening to music, or talking (no laptop). At noon and at 17:30, subjects were given a sandwich. The working area in front of the subject was slightly tilted (45°) to ascertain a more vertical gaze direction. All subjects underwent two different lighting environments during the afternoon in a cross-over design: a standard office fluorescent polychromatic white light source [3700 K; averaged illuminance in a vertical plane at the subjects' eye level (E_v) was 176.3 ± 1.3 lx; mean \pm SEM], and the second one mainly under daylight. In the daylight condition, target illuminance was maintained at approximately 1000 lx in a vertical plane at the subjects' eye level (E_v). Daylight entered the room via the upper part of a southern facade equipped with anidolic daylighting systems (Scartezzini & Courret, 2002). The lower blinds were fully closed to avoid any bias due to vertical outside view through the conventional windows. Target light illuminance during the daytime exposure was controlled every 30 min using a spectroradiometer (specbos, JETI, Jena, Germany) and if necessary reduced by closing additional blinds of the upper windows or by switching on the fluorescent polychromatic white light source (3700 K), when E_v dropped below 1000 lx. The latter was necessary with overcast skies or in the late afternoon hours; for example, after 17:00 for almost all DL study days because of the season (fall/winter). During the six afternoon hours of the DL condition, there was an average illuminance (E_v) of 984.8 ± 85.5 lx (mean \pm SEM).

After the 6 hours of experimental light exposure, subjects were seated in a different laboratory room with only dim light (<6 lx)

for the next 2 hours. They were asked to produce a saliva sample every 30 min for hormonal analyses. Saliva samples for cortisol and melatonin assays were immediately stored at 4 °C, and frozen at -20 °C after centrifugation. Upon study completion samples were sent for radioimmunoassays to the Centre Hospitalier Universitaire Vaudois (CHUV), Lausanne (Switzerland). Detection threshold for melatonin was 0.2 pg/ml (Bühlmann Laboratories, Schönenbuch, Switzerland), with intra- and interassay coefficients which were lower than 5.8% and 11.4%, respectively. Detection threshold for cortisol was 1.6 pg/ml (Assay COAT-A COUNT, code TKC01, Siemens Health Diagnostics Inc., Los Angeles, CA). Intra- and interassay coefficients for cortisol were lower than 10.6% and 12.8%, respectively. Only samples of salivary cortisol and melatonin concentrations that were above detectable threshold were included in the analysis.

Throughout the eight hours of the study, subjects assessed their subjective sleepiness on the 9-item Karolinska Sleepiness Scale (KSS) every 30 min, their subjective well-being, mood, physical wellness, as well as visual comfort on visual analogue scales (VAS). Here we only report the results from the KSS and compared them between the two lighting conditions; two missing values were linearly interpolated.

In the evening after 18:00 subjects completed an n-back task every 30 min, a task which is known to demand executive control processes (Jaeggi et al., 2003). In this task, participants are presented with a sequence of visual stimuli (abstract shapes; Jaeggi et al., 2010). They are required to respond whenever the current stimulus is the same as *n*-positions back in the sequence. Before starting, subjects performed a practice run for both load levels. We used two load levels; that is, 2-back and 3-back. Each n-back session started with three runs of the (easier) 2-back version followed by three runs of the (more difficult) 3-back test version. Each run consisted of 20 + *n* trials. Accuracy (*pr*, calculated as hits minus false alarms), as well as false alarms per se, and reaction time (RT) for correct trials, averaged for each load level, were used as outcome variables.

Statistics

Statistical analysis was performed by using the software packages SAS, Version 9.2 (SAS Institute Inc., Cary, NC) and Statistica, Version 9 (STATISTICA for Windows, Tulsa, OK). Repeated analyses of variance (rANOVAs) were performed with a general linear regression model (GLM) and using the factors *load* (2-back, 3-back), *gender*, *condition* (daylight = DL, artificial light = AL), and *time* (sessions in the evening) and *group* (AL or DL on the first day). For analysis of cortisol and melatonin concentrations, a mixed linear regression model (PROC MIXED) was used for values above detectable threshold. Averaged data per subject from subjective sleepiness assessments (KSS) and n-back tasks were analyzed on absolute or relative data (deviation from mean). For RTs, we analyzed the median, the 10% fastest and the 10% slowest RT. All *p* values derived from rANOVAs were based on Huynh-Feldt's (H-F) corrected degrees of freedom (significance level: *p* < .05). For post hoc tests, we used Duncan's multiple range or *t* tests; *p* values were adjusted for multiple comparisons.

Results

Salivary Cortisol and Melatonin

Salivary samples for cortisol and melatonin were obtained under dim light conditions from 28 subjects (from the last subject we did not ask for saliva samples). As expected, cortisol concentrations in the early evening were on the decreasing limb at this time of day (main effect of time; $F(4, 204) = 34.1$; $p < .05$). Averaged salivary cortisol concentrations were 3.56 ± 1.74 pg/ml after AL and 3.61 ± 1.82 pg/ml after DL (mean \pm SD; $n = 26$, because salivary cortisol concentration was below threshold for two subjects). There was no difference in evening cortisol concentrations after the two lighting conditions ($p = .82$).

Dim light salivary concentrations of melatonin in the early evening hours were all ≤ 1 pg/ml, except for two subjects where melatonin concentrations increased slightly above 1pg/ml in the last hour of the study (to maximal 7 pg/ml) after both lighting conditions, indicating the onset of melatonin secretion. Averaged dim light salivary melatonin values in the evening were 0.77 ± 1.2 pg/ml after AL and 0.76 ± 1.3 pg/ml after DL (mean \pm SD; $n = 15$), averaged for those subjects who had melatonin concentrations above detectable threshold. There was no difference in salivary melatonin concentration between both light conditions ($p = .84$).

Subjective Sleepiness

For subjective sleepiness there was no effect of order or gender ($F(1, 25) < 2.8$; $p > .1$; four-way rANOVA) across the entire study duration, therefore these factors were not further included as covariates. Subjective sleepiness (KSS) during the afternoon did not differ between the two study days ($F(1, 28) = 0.52$; $p = .48$; two-way rANOVA), and was in average the same for both lighting conditions in the afternoon (AL: mean 4.1 ± 0.5 ; DL 4.1 ± 0.6 mean \pm SD; $p > .9$; two-way rANOVA; main effect of condition). There was a significant change over time during the afternoon for both lighting conditions, such that compared to the first 30 min, subjects became significantly sleepier in the course of the afternoon ($F(12, 336) = 12.4$; $p < .05$; main effect of time; Figure 1a). During DL, subjective sleepiness increased by 24% from 3.03 ± 0.21 to 3.76 ± 0.30 (mean \pm SEM). For AL, subjective sleepiness increased by 33% from 3.07 ± 0.25 to 4.09 ± 0.28 .

Concerning overall subjective sleepiness ratings in the evening (e.g., under the dim light condition), we found that those subjects, who had been exposed to AL during the afternoon were not sleepier compared to those who were exposed to DL (main effect of condition; $F(1, 28) = 3.2$; $p = .08$; two-way rANOVA) and there was no significant interaction with the factors condition \times time ($p > .33$) or between the two study days ($p = .36$).

In a next step we expressed evening sleepiness relative to the averaged afternoon ratings for each lighting condition separately (Figure 1b). Compared to mean sleepiness ratings (KSS) in the afternoon, subjects were significantly more alert at the beginning of the dim light session in the evening after the DL condition (*t* test to mean; adjusted $p = .04$; $t = 2.1$; \pm 95% interval: 0.07–0.01). After the AL condition, subjects felt significantly sleepier toward the end of the study, e.g., after 2 hours in dim light, when compared to mean sleepiness ratings in the afternoon (Figure 1b; $p = .006$; $t = -2.9$; \pm 95% interval: 0.08–0.31).

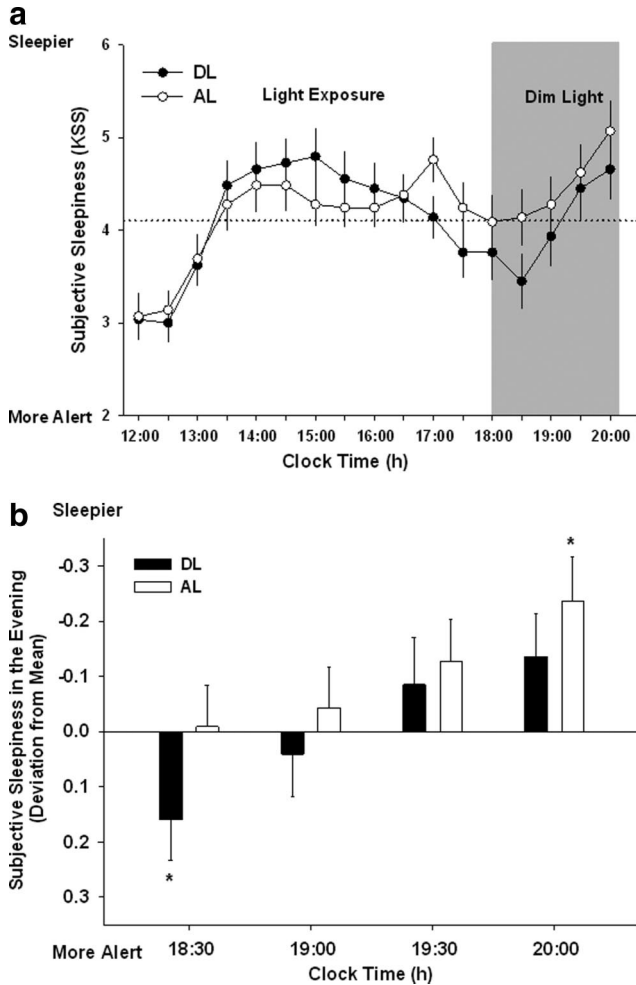


Figure 1. **a:** Time course of subjective sleepiness (KSS) across the study. White background = light exposure; gray background = dim light ($< 6lx$). Black circles = daylight (DL); white circles = artificial light (AL). $N = 29$; mean \pm SEM. The dotted black line indicates the averaged afternoon value for both light conditions. **b:** Dim light subjective sleepiness ratings expressed as deviation from mean in the afternoon. $N = 29$; mean \pm SEM; black bars = DL; white bars = AL. Averaged values in the afternoon = 0 (black line). * = significant differences of the respective condition compared to the afternoon ($p < 0.05$).

In order to test whether better cognitive performance was associated with lower sleepiness ratings, we performed a correlation analysis (Pearson's correlation) with the performance results from the averaged n-back tasks (2- and 3-back), and mean KSS ratings in the evening (Figure 2). For this purpose, accuracy values (hits minus false alarms) were averaged per subject for both task versions and across all test sessions (8 tests per subject). Subjective sleepiness ratings were averaged per subject across all sleepiness ratings in the evenings (8 ratings per subject). We found that lower sleepiness ratings were significantly correlated with better performance in the evening ($r = -0.5$; $p = .006$).

Cognitive Performance

Overall, we found a significant interaction for accuracy (hits minus false alarms) with the factors gender and group and the

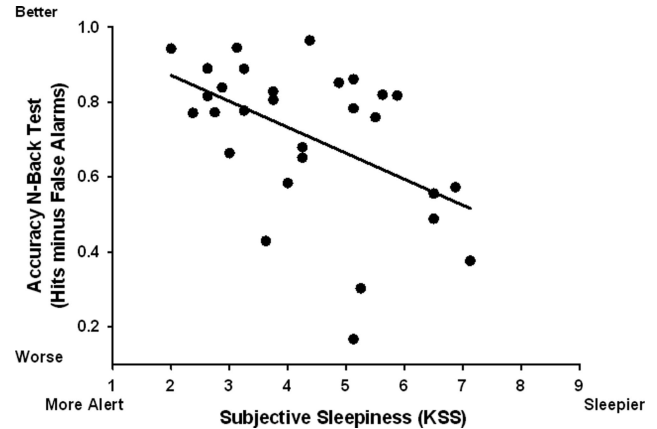


Figure 2. Scatter plot (Pearson's Correlation) for n-back tasks and subjective sleepiness ratings. For n-back tasks, accuracy values (hits minus false alarms) were averaged per subject across all test sessions ($= 8$ test sessions per subject); subjective sleepiness ratings were averaged per subject across all sleepiness ratings in the evenings ($= 8$ ratings per subject). The black line indicates the regression line, $r = -0.5$ ($p = 0.006$; $N = 29$).

repeated factors load, condition, and time ($F(3, 75) = 2.9$; $p = .04$). Significant main effects were such that accuracy for the 2-back task was higher compared to the 3-back task ($F(1, 25) = 80.4$; $p < .05$; main effect of load), and that subjects in the group who started the study with AL performed overall better than the others ($F(1, 25) = 7.8$; $p < .05$; main effect of group), independent of condition.

We then analyzed the two task loads separately and found that in the 2-back task, participants performed significantly better after the DL than the AL condition, (DL accuracy: $83.6\% \pm 4\%$; AL accuracy: $80.3\% \pm 3\%$; mean \pm SEM; $F(1, 27) = 5.4$; $p < .05$; main effect of condition, Figure 3). Furthermore, those subjects who started the study with AL performed significantly better than those who started the study with DL ($F(1, 27) = 6.7$; $p < .05$; main effect of group). For the 3-back task, there was no significant difference between the two lighting conditions overall ($F(1, 27) =$

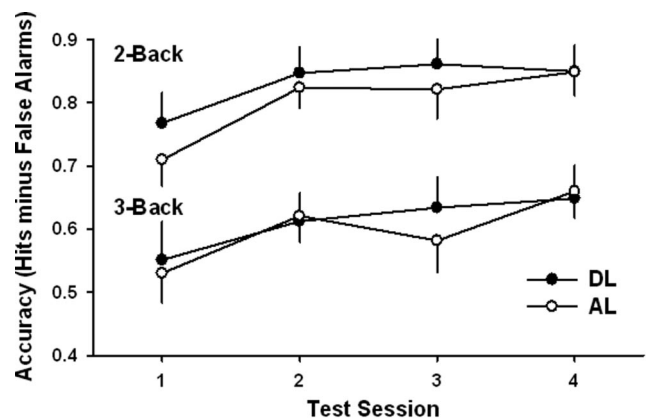


Figure 3. Accuracy for 2-back and 3-back test sessions 1–4 (black circles = DL; white circles = AL); $N = 29$; mean \pm SEM; main effect of condition for the 2-back task ($p < 0.05$).

0.6; $p = .5$). For both task loads, we found a significant improvement of accuracy in the course of the evening ($F(3, 81) > 8.3$; $p < .05$; main effect of time) and a significant interaction with the factors group \times condition \times time (3-way rANOVA: $F(3, 81) > 2.9$; $p < .05$). Post hoc tests revealed similar performance on Day 1 in the 2- and 3-back task ($F(1, 27) = 3.6$; $p = .07$ and $F(1, 27) = 2.6$; $p = .12$, respectively). Even though both groups improved on the second study day ($F(1, 27) > 24.8$; $p < .05$; main effect of day), there was a significant better performance on the second day for subjects who were exposed to DL during the afternoon in both n-back task loads ($F(1, 27) > 4.2$; $p < .05$; Figures 4a and 4b).

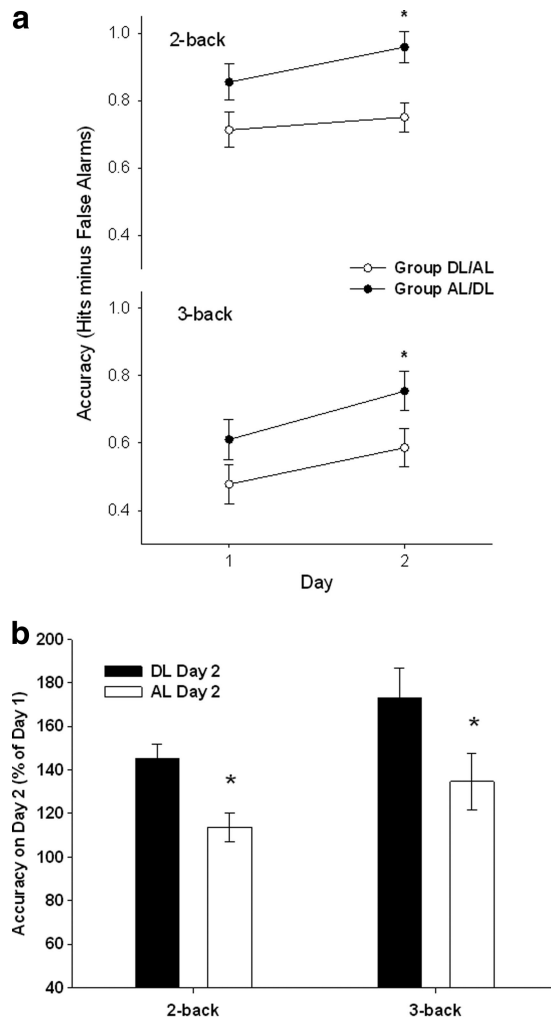


Figure 4. **a:** Accuracy (hits minus false alarms) during the cognitive performance tests for the 2-back (upper panel) and the 3-back tests (lower panel). Averaged values for Day 1 and 2 are shown for both groups. Black circles indicate the group who had AL on Day 1 and DL on Day 2. White circles are showing the group who started with DL and had AL on Day 2. * = significant differences between the two lighting conditions on Day 2 ($p < 0.05$); $N = 29$; mean \pm SEM. **b:** Accuracy (hits minus false alarms) during the cognitive performance tests for the 2-back (left) and the 3-back tests (right) for Day 2. Mean values per evening were expressed as percentage of the first assessment in the evening of Day 1. Black bars = DL; white bars = AL; $N = 29$; mean \pm SEM; (* = $p < 0.05$).

These results remained significant even when we only included the best performing subjects (i.e., with an accuracy greater than 80% in the 2-back task on the first day), which was the case for 8 and 10 subjects respectively, from both groups. With these well performing subjects, we still found significantly higher accuracy for the 2-back test on the second day for those subjects who were previously been exposed to DL ($F(1, 16) = 32.9$; $p < .05$).

For RTs subjects had significantly longer RTs for the 3-back than the 2-back tasks ($F(1, 27) = 18.7$; $p < .05$; 3-back: 811 ± 46 ms; 2-back: $702 \text{ ms} \pm 38 \text{ ms}$; mean \pm SEM; three missing values were linearly interpolated). In addition to the median RT, we also looked at the 10% slowest and the 10% fastest RT; however, we found no difference between the two lighting conditions in neither of those measures (all $p > .1$). For false alarms, subjects committed fewer false alarms in the 2-back compared with the 3-back task (2-back: 1.7 ± 0.4 ; 3-back: 3.6 ± 0.5 ; mean \pm SEM; main effect of load; $F(1, 27) = 35.4$; $p < .05$). In addition, there was a significant interaction with the factors time \times condition \times group for the 2-back task ($F(3, 81) = 9.5$; and $p < .05$). Post hoc analysis for the 2-back task showed a comparable false alarm rate between the two conditions on the first day (DL = 2.9 ± 0.7 vs. AL = 1.4 ± 0.7 , respectively; mean \pm SEM; $F(1, 27) = 2.1$; $p = .2$), but significant more false alarms on Day 2 for those subjects who received AL on the second day (AL: 1.9 ± 0.4 ; DL 0.7 ± 0.4 ; mean \pm SEM; $F(1, 27) = 4.3$; $p < .05$).

Discussion

In the evening when the cognitive performance testing took place, salivary cortisol secretion did not vary between the two prior light exposure conditions, and no salivary melatonin secretion was above threshold in all but two subjects. Compared to the afternoon, subjects who had DL were significantly more alert at the beginning of the evening, and subjects who were exposed to AL were significantly sleepier at the end of the evening. There was no difference in cognitive performance in the evenings of the first day, but on the second day, significantly better evening performance after DL exposure than compared to AL, for both task versions (2- and 3-back).

It has been widely accepted that endogenous cortisol concentration is a reliable circadian phase marker of the biological clock (Jung et al., 2010) and is also sensitive to acute phase resetting capacities by different lighting conditions. Previous studies reported that changes in response to light exposure were greatest in the early morning hours when cortisol concentrations are highest (Scheer & Buijs, 1999). Differences of prior light history did not show up in differences in cortisol concentrations during the day or the evening (Leproult, Van Reeth, Byrne, Sturis, & Van Cauter, 1997; Rüger et al., 2006), most likely due to already low endogenous cortisol concentrations. We also did not control for the subjects' prior light exposure during the morning hours before entering the laboratory.

Our study design was aimed to test cognitive performance and sleepiness in the early evening; that is, before the onset of melatonin secretion. As expected, salivary melatonin concentrations were not detectable in most of the subjects, documenting that all of them were entrained to a regular 24-h day. In entrained subjects, dim light melatonin onset starts later, approximately 2–3 hours before habitual sleep time (Benloucif et al., 2008), which occurred

after our study ended in the second part of the evening. Thus, our differences in subjective sleepiness and cognitive performance are rather not impacted by the sleepiness-inducing effect of endogenous melatonin secretion in the evening. However, we cannot exclude any phase shifting effects since we did not measure circadian phase by dim light melatonin onset later in the evening.

Subjective alertness is under strong control of the endogenous biological clock and, in addition, varies with prior duration of wakefulness. It is the interaction of these two processes (Borbély, 1982; Dijk & Czeisler, 1994) that allows a consolidated bout of wakefulness during daytime and an approximate 8-hr sleep episode during the night in humans. In a dose-response curve with different light intensities an approximate vertical illuminance between 90–180 lx was shown to be sufficient to induce 50% of the maximal light-induced change of alertness during nighttime (Cajochen et al., 2000). As stated, those light exposures were performed during nighttime and followed a dim light adaptation of several hours. Thus, even though the light intensity of that study is comparable with the illuminance measured in our AL condition (which is similar to an artificial standard room illumination), we cannot say that our subjects were only at 50% of their peak level of alertness; however, they were certainly less alert during the afternoon than at the beginning of the study. Rüter and colleagues exposed healthy young subjects from noon to 16:00 to bright light of 5000 lx in a vertical direction. They found a significant decrease of subjective sleepiness (KSS), when compared to dim light (<10 lx) (Rüter et al., 2006). The vertical illuminance in their bright light condition was much higher than the AL and DL condition in our own study. Nevertheless, the exerted alerting responses during daytime light exposures are comparable with the responses of our participants (around 4 on the 9-item KSS scale), indicating that both lighting conditions in our study were sufficient to maintain daytime alertness. We only observed significant changes in sleepiness in the evening hours when subjects were placed under dim light. In the two evening hours in dim light, and without the presence of the acute alerting light stimulus, the differences on progressing sleepiness became more overt and affected its time course in the evening hours differently, depending on prior light intensity (and perhaps spectral composition of light). We can only speculate that the two different light intensities during the afternoon resulted in a different magnitude of brain activation, which in turn led to an earlier occurrence of sleepiness in the group that has been exposed to lower light levels (AL). Thus, specific cortical activations during the afternoon led to a sustained effect in the evening and concomitantly changed the time course of sleepiness. There is some evidence in the literature supporting the argument of such a sustained light response even beyond light exposure. For example, Lockley and colleagues (2006) demonstrated that the greater alerting effect of exposure to monochromatic blue light (at 460 nm) compared to dim light lasted for more than 1 hour beyond the actual light exposure. Further, Sletten and colleagues reported sustained alerting responses to monochromatic blue light that were detectable until 5 hrs after light exposure when compared to dim light levels (Sletten, Revell, Middleton, Lederle, & Skene, 2009).

Nonvisual brain activity during cognitive performance tasks can be changed by light as it was demonstrated with several functional MRI (fMRI) and PET studies (Perrin et al., 2004; Vandewalle et al., 2006; Vandewalle, Gais et al., 2007; Vandewalle, Maquet, & Dijk, 2009; Vandewalle, Schmidt et al., 2007). These nonvisual

brain responses to cognitive tasks were modulated by light in a wavelength, duration, and intensity-dependent manner with temporal activity changes: early activation (after 1–17 min) could be detected in subcortical structures (brainstem, thalamus, hypothalamus), followed by activity changes in cortical areas (after 18–20 min) (Vandewalle et al., 2009). Several cortical brain areas involved in the regulation of attention showed modulations of activity in response to light such as the left intraparietal sulcus and the superior parietal as well as the prefrontal cortices. Neuroimaging studies also found light-dependent activity changes in brain areas involved in working memory, such as the middle frontal gyrus, the supramarginal gyrus, and the intraparietal sulcus (Perrin et al., 2004; Vandewalle et al., 2006; Vandewalle, Gais et al., 2007; Vandewalle et al., 2009; Vandewalle, Schmidt et al., 2007). In all the aforementioned studies, the accuracy during task performance was aimed to be similar between experimental light conditions in order to quantify the different effects of light on brain activation. We conclude from our study that the observed changes in accuracy during the n-back task after brighter DL exposures can be attributed to differential cortical responses as a function of light intensity, and in addition by increased levels of alertness and attention. These effects lasted several hours beyond light exposure and suggest that melanopsin-dependent pathways were involved.

There was also a significant correlation between lower subjective sleepiness and better cognitive performance, which is consistent with previous studies where higher subjective alertness produced shorter RTs in a sustained attention task (Lockley et al., 2006; Phipps-Nelson et al., 2003). Brain activating processes via the ascending reticular activating system (ARAS; Moruzzi & Magoun, 1949) are also related to higher cognitive performance (Vandewalle et al., 2009). Nevertheless, to date it is not clear if higher cognitive performance is solely dependent on activation of arousal-related brain areas. A near-infrared spectroscopic study revealed characteristics to overcome sleepiness during the n-back working memory task, which went beyond the traditionally proposed attention-related networks (Honma, Soshi, Kim, & Kuriyama, 2010). It seems that under certain cognitive demands, the brain recruits additional resources that can be manifested either as larger responses in activated brain regions or in the use of additional brain regions that are normally not involved with this task response, as already shown with total sleep deprivation and varying task load levels (Drummond, Brown, Salamat, & Gillin, 2004; Jaeggi et al., 2003). And lastly, there might be a selective, light-sensitive activation process, which also involves higher order cortical areas (in addition to the brainstem), such as the prefrontal cortex, the premotor cortex, the parietal cortex, and the thalamus, as hypothesized in a functional MRI study (Vandewalle et al., 2009).

Better accuracy on the second day after the DL condition was also associated with fewer false alarms for the 2-back task. This result raises the question whether learning and practicing abilities of a new working memory task (Day 1) require different neuronal networks than for the performing abilities of the task on Day 2. Are the neuronal networks involved on Day 1 executive demand less sensitive to previous lighting conditions? Could any putative light effects on the Day 1 be “masked” by excessive mental efforts, when compared to brain networks involved in the “practiced” task performance on Day 2? In favor of this argument is the fact that the significant differences in cognitive performance between both

lighting conditions on the second day remained, even if we only included the best performing subjects; that is, those with accuracy greater than 80% in the 2-back task on the first day.

It has been reported that with a greater cognitive load, prefrontal brain areas are supported to a greater extent by intraparietal and other brain structures in their performance (Vandewalle et al., 2009). Considering this result, one could conclude that working memory tasks, which require a great level of attentional control, should be sensitive to prior light history. Such a relationship could be crucial for workers requiring high attention levels and executive functioning, such as bus drivers, industrial workers in sensitive areas, or air-traffic control.

A limitation of our study is the fact that the brighter, mainly daylighting condition, had a different spectral composition than the AL condition, and thus, we were not able to distinguish between effects due to differences in spectral composition or illuminance alone for the interpretation of our results. This is why future studies should also address the effects of different spectra at equal light flux, as in the study with blue-enriched versus white polychromatic light exposure (Viola et al., 2008), or where blue-enriched artificial lighting competed with evening daylight exposure and prevented adaptation to changes in seasonal day length (Vetter, Juda, Lang, Wojtysiak, & Roenneberg, 2011). Finally, more studies are needed that deal with natural, highly dynamic lighting situations, because these are the most prevailing lighting conditions at workplaces during the day. Increased knowledge gained from such daylighting studies may also allow better designs of electric lighting with beneficial effects related to nonvisual functions of light quality.

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