Light of both high and low melanopic illuminance exerts positive effects on attention and alertness during daytime

Louise Bruland Bjerrum[1]*, Endre Visted[1], Inger Hilde Nordhus[1], Berge Osnes[1], Bjørn Bjorvatn[2,3], Oda Bugge Kambestad[1], Malika Elise Hansen[1], Lin Sørensen[4], & Elisabeth Flo-Groeneboom[1]

[1]Department of Clinical Psychology, University of Bergen, Norway

[2]Department of Global Public Health and Primary Care, University of Bergen, Norway

[3]Norwegian Competence Center for Sleep Disorders, Haukeland University Hospital, Norway

[4]Department of Biological and Medical Psychology, University of Bergen, Norway

*Corresponding author. Email: louise.bjerrum@uib.no.

Abstract

Light exposure during the day exerts acute effects on attention, such as how alert and ready a person is for solving problems and goal-oriented behavior. However, to increase the understanding of how different light conditions during daytime affect our attention, there is a need for more studies. The current study, using a sample of healthy, young adults (*N* = 39; age = 21.7 ± 2.6, 61.5% females), tested the acute effects of daytime exposure (09:00-11:00) to four artificial light conditions on attention and alertness with the Psychomotor Vigilance Task (PVT). The PVT was administered three times in short-wavelength "blue" light [SWL, high melanopic illuminance], long-wavelength "red" light [LWL, low melanopic illuminance], and bright white light [BWL] of high correlated color temperature, and white dim light [DL] as the control condition. PVT measures included fluctuations in attention, quantified as intra-individual Reaction Time (RT) variability and the number of lapses; mean RT; and optimum response capability (10% fastest RTs). Compared to DL, participants had significantly fewer lapses and faster mean RT during SWL and LWL, and they enhanced their optimum response capability during LWL. There were no significant effects of BWL, and light did not appear to have effects on RT variability. Surprisingly, SWL was not superior to LWL. Hence, our results

suggest that light, irrespective of melanopic illuminance, has the potential to increase alertness and attention during daytime.

Introduction

Impaired alertness is a common problem in everyday life and can arise from inadequate sleep related to work schedules and various societal/domestic demands. Irrespective of the cause, low alertness levels can be a risk factor for accidents and reduced performance in occupational and operational settings, especially during night shifts[1–7]. Exposure to light has been tested as an intervention to optimize alertness during night shifts, however, most of these interventions have involved exposure to white light[8–10]. It is therefore of interest to better understand how different light conditions affect aspects of alertness, also during the day, to enhance cognitive performance.

Light is involved in a range of so-called Non-Image Forming (NIF) responses, including acute effects on alertness[11,12], melatonin suppression[13–15], pupil constriction[16,17], and synchronization of the "master" circadian clock in the brain to the environmental light-dark cycle[18]. NIF responses are mainly driven by intrinsically photosensitive Retinal Ganglion Cells (ipRGCs), a small subset of photoreceptors in the retina[19]. ipRGCs contain the photopigment melanopsin that is maximally sensitive to short-wavelength light (SWL) with a peak at ~ 480 nm[20,21]. SWL with a narrow bandwidth (that is, with a narrow peak in some part of the visible electromagnetic spectrum) will appear blue to the human eye. Similarly, medium-wavelength light (MWL, with a peak spectral wavelength at ~ 550 nm) will appear green, and long-wavelength light (LWL, with a peak spectral wavelength at ~ 630 nm) will appear red. Polychromatic white light will also activate melanopsin, especially if the white light is bright enough, and/or "cool". "Cool" white light is often enriched in shorter wavelengths, resulting in high Correlated Color Temperature (CCT, measured in kelvin (K)), whereas "warm" light is enriched in longer wavelengths, resulting in lower CCT. Light with high proportions of short wavelengths will typically also have a high melanopic-Equivalent Daylight Illuminance (m-EDI). This metric that has been proposed as the preferred metric (over the "traditional" photopic illuminance metric) when quantifying the biological effects of light[22,23]. Given the role of light in various NIF responses it is crucial to understand how different light conditions influence attention and alertness. Alertness, a subfunction of attention, follows a circadian (~ 24 hour) rhythm, with low alertness levels immediately upon awakening, followed by increased and rather stable levels throughout the day and subsequent lower levels in the evening and at night[24]. Being alert and attentive is associated with the functioning of the alerting network, one of the three main attention networks of the human brain[25]. Adequate alertness levels throughout the day enable high sensitivity to incoming stimuli and facilitate more complex, cognitive tasks[26]. Systematic reviews have shown that exposure to SWL, bright white light (BWL), and white light of high m-EDI during the day can increase neurobehavioral alertness, however, other studies report no significant effects (reviewed in[27–29]). Furthermore,

some studies have shown that exposure to LWL can have positive effects on electroencephalography (EEG) markers of alertness[11,30,31]. Importantly, though, acute effects of light on neurobehavioral alertness can be influenced and confounded by a range of factors, such as chronotype (inter-individual differences in preferred sleep and wake timing, e.g., whether one is a "morning lark" or an "evening owl")[32] and various sleep-related variables. Poor sleep quality and sleep restriction (curtailed sleep duration) have been linked to alertness deficits in healthy individuals[33–36], however, light exposure has the potential to counteract such deficits[37–39]. Furthermore, seasonal changes in ambient light levels can also affect NIF responses to light, probably due to changes in light sensitivity[40,41]. Therefore, it is important to take these factors into consideration when assessing the alerting effects of light.

The Psychomotor Vigilance Task (PVT) is a high signal-load reaction time (RT) task widely used to assess alertness in laboratory contexts. It has minor learning effects, making it ideal for repeated measures[42]. The most commonly reported PVT metrics are mean reaction time (RT) and the number of lapses in attention (often quantified as RTs ≥ 500 ms). A less commonly reported PVT metric is the 10% fastest RTs, reflecting the most optimum responses on the task[43]. Studies using the PVT to assess alertness in different light conditions have reported faster mean RT and fewer lapses during SWL ("blue")[44], bright white light[12,45,46] and white light of high m-EDI[47]. However, other studies report no significant effects[48–54]. Additionally, most studies report no significant effects of white light on the 10% fastest RTs[12,45,48,50,51,53,55–58]. Even though the acute effects of LWL ("red") on EEG markers of alertness/drowsiness have been described in the literature to some extent[11,30,31,59], the literature on the acute effects of LWL on alertness measured with RT-based tasks such as the PVT or other sustained attention tasks is scarce and inconclusive[31,54]. Also, it remains unknown whether the 10% fastest RTs in particular can be modulated by exposure to narrow bandwidth lights during the day. Finally, relatively few studies have assessed light's impact on fatigue over time in testing, a factor that may increase RTs across PVT sessions[12,46,48,52].

In sum, research on the acute effects of light during daytime on neurobehavioral alertness is inconclusive. Importantly, previous literature on the NIF acute effects of light on RT-based alertness have focused on central tendency measures, reflecting average performance across individuals. To our knowledge, it remains to be tested whether different types of artificial light can exert acute effects on alertness and attention measured at an intra-individual level in terms of RT variability (RTV). As RTV on the PVT is underreported in the literature, it is of interest to include this outcome to get a more nuanced picture of how light acutely impacts attentional fluctuations. Also, there is limited knowledge on how chronotype and season might affect neurobehavioral performance during light exposure. The overall aim of the present study was therefore to assess the impact of daytime exposure to different artificial light conditions on neurobehavioral alertness in healthy, young adults. By assessing not only the acute effects of different light conditions on central tendency measures, this study also tests the acute effects of light on intra-individual RTV, thereby filling a gap in the

literature. Hypotheses were pre-registered at OSF (https://osf.io/m7gfh). Based on previous research and theory on the NIF acute effects of light, we hypothesized that:

- Short-wavelength ("blue") light (SWL), long-wavelength ("red") light (LWL) and bright white light (BWL), compared to dim light (DL), will reduce fluctuations in attention (quantified as intra-individual RT variability and the number of lapses) and overall mean RT on the PVT.
- SWL, LWL, and BWL, compared to DL, will not affect optimum response capability (quantified as the mean of the 10% fastest RTs).

As the differential effects between SWL, LWL, and BWL on alertness and attention are inconclusive in the literature[27], we tested the following explorative hypothesis:

- SWL will have a superior effect on intra-individual RTV, lapses and mean RT, compared to LWL, and BWL will have a superior effect on intra-individual RTV, lapses and mean RT, compared to LWL.

Last, we also hypothesized, exploratively, that:

- Participants tested in fall and winter will show stronger responses to light than participants tested in spring and summer.
- Individuals with a 'morning' chronotype or 'intermediate' chronotype will perform better than 'evening' chronotypes, and 'evening' chronotypes will benefit more from light with high m-EDI compared to DL, relative to 'morning' and 'intermediate' chronotypes.

Methods

Study design and setting

This study used a within-subjects repeated measurements experimental design to test the acute effects of daytime exposure to different artificial light conditions on alertness and attention in healthy, young adults. Data collection was conducted from November 2021 to October 2023, at a high latitude (60.39° N) in a 23 m^2 laboratory with no windows. The laboratory was equipped with 20 60x60 ceiling-mounted Light Emitting Diode (LED) luminaires (Glamox AS, Norway) and nine working stations in total, equipped with a desk, chair, a PC, keyboard and computer mouse. All computer screens had an overlay screen foil blocking wavelengths < 520 nm (Metolight SFG-10, Asmetec, Germany), to avoid potential alerting effects resulting from light radiating from the screens. Additional information about the laboratory setup and a graphical overview of the laboratory is provided in Supplementary Materials S1 and Fig. S1, respectively.

Participants

Healthy, young adults (≤ 40 years old) were recruited in lectures at the University of Bergen, Norway, and through online and on-campus posters. Based on a screening procedure, participants were included if they had normal or corrected-to-normal vision. Participants were excluded if they were colorblind (as indicated with Isihara's Test for Color Deficiency), had traveled across three time zones within the last three weeks, had a severe psychiatric disorder (as indicated by the Symptom Check List-90 and module C from Mini International Neuropsychiatric Interview, probing symptoms of mania), or a severe medical disorder.

Procedures

Participants underwent one week of baseline at home, followed by four in-laboratory test sessions occurring from 08:00 to 11:00 on separate days during a two-week period. One light condition was presented in each session, in a block-stratified randomized cross-balanced order for each participant. There was at least one day in between sessions. During the entire three-week study period, participants were instructed to maintain a regular sleep-wake schedule, including on weekends, however, they were not required to spend a predefined number of hours in bed each night. Sleep was measured with sleep diaries and activity watches (Actiwatch Spectrum Plus, Philips Respironics, Inc., United States) worn on participants' non-dominant hands. On the morning of scheduled test sessions, participants were instructed to wear short-wavelength light-blocking glasses (Uvex, Honeywell International, Inc., United States) immediately upon awakening to ensure that i) there were no SWL-induced alerting effects of light in the environment prior to assessment in the laboratory, and ii) to reduce variation in light history between participants and seasons. Prior to entering the laboratory at 08:00, participants were allowed to consume their habitual morning dosage of caffeine, however, during in-laboratory testing, no caffeine consumption nor nicotine use was allowed.

Participants arrived at the laboratory at 08:00 and were maintained in warm-white dim light (DL, m-EDI = 4.8±6.2 lux (lx)) for one hour, followed by 30 minutes of adaptation to one of the three experimental light conditions or the control light condition. At the beginning of the one-hour exposure to warm-white DL, participants were fitted with two electrocardiography (ECG) electrodes to measure resting heart-rate variability (HRV). Resting HRV was sampled for 10 minutes at approximately 08:40. At approximately 08:50, the given experimental light condition increased gradually in illuminance over the course of 10 minutes to limit eye strain. In between ECG mounting and the HRV assessment, and during the 30 minutes of light adaptation, participants sat comfortably in a chair at their designated workstation, talking with the other participants and the experimenter. A small snack was provided during light adaptation, whereas water was available during the entire test session. Pupils were not pharmacologically dilated prior to light exposure. After light adaptation, a second resting HRV was sampled for 10 minutes, followed by the administration of neurobehavioral tasks for approx. 1.5 hour during exposure to different artificial light conditions (see Fig. 1). The light conditions were three experimental conditions of narrow bandwidth SWL ("blue", λ_{max} = 455 nm, m-EDI = 1441.8±35.2 lx), narrow bandwidth LWL

("red", λ_{max} = 625 nm, m-EDI = 3.8±1.3 lx), and BWL (m-EDI = 1155.8±17.6 lx, CCT = 8035.7±42.8 K), and one control light condition of white DL (m-EDI = 9.7±6.4 lx). Hence, SWL and BWL were both of relatively high m-EDI, whereas the LWL condition had a low m-EDI. SWL and LWL were matched on photon irradiance (= log 18.8/m^2/s). Photoreceptor-weighted (α-opic) light quantities were calculated using the open-access- and source web platform *luox*[22,60]. Photoreceptor-weighted light quantities, spectral power distribution graphs, and spectral irradiance raw data are available in Supplementary Materials S2 (Table S2.1, Fig. S2.2, and Table S.2.3, respectively). The three experimental light conditions were delivered through the ceiling-mounted LED luminaires. In the DL control condition, all LED luminaires were off; the only light source in the room was light radiating from the computer screens. During the one-hour exposure to warm-white DL from 08:00 to 09:00, preceding light adaptation, DL was delivered through six portable Philips Hue Go lamps situated behind the computer screen at each workstation, in an upward position facing away from the participants. At each workstation, light stimuli were measured with a calibrated spectroradiometer (GL Spectis 1.0 T Flicker, GL Optic, Poland) at eye level (vertically, 120 cm above the floor), ~90 cm horizontally from the computer screen in the direction of gaze (corresponding to the approximate seating of participants) with the screens turned on. The light measurements were performed approximately 30 minutes after the onset of the LED luminaires to allow the luminaires to adjust in temperature.

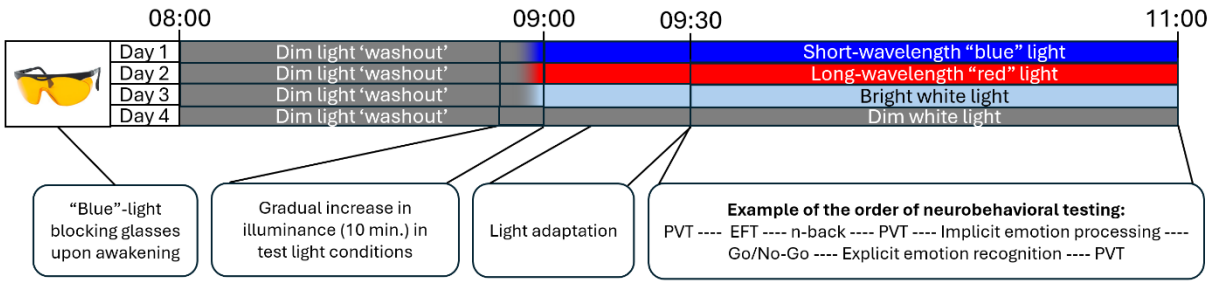

Figure 1. Overview of experimental design. From 09:30 to approximately 11:00, participants performed a series of neurobehavioral tests assessing alertness (Psychomotor Vigilance Task (PVT)), cognitive control (Eriksen Flanker Task (EFT)), working memory (n-back) and aspects of emotion processing (implicit and explicit emotion recognition and a Go/No-Go task with emotional stimuli). Results from the EFT, n-back. and emotion tasks will be reported in future publications. The presentation order of light conditions and the order of cognitive vs. emotion-related tests were randomized and cross-balanced within groups of participants, however, not for the PVT, as this task was administered in three blocks at fixed intervals throughout light exposure (at ~ 09:40, ~ 10:15, and ~ 10:50).

Ethics

Participants provided written informed consent before participation and received 1000 NOK (~ 94 USD) after completing the study. Ethics approval was provided by the Regional Committees for Medical and Health Research Ethics. All procedures contributing to this work comply with the Declaration of Helsinki.

Measures

Alertness

Alertness was assessed three times in each of the four light conditions (block 1-3, see Fig. 1) with a five-minute computerized version of the PVT[42,61] administered through E-Prime 3.0[62]. Participants monitored a red rectangular box on a white background. When a counting timer (stimulus, in black) appeared inside the box and started counting, participants were instructed to press the space bar as quickly as possible. The stimulus was presented at random intervals ranging from 2 to 7 s, and 1 s feedback on RT was provided after each trial. RTs < 100 ms were considered false starts. Five practice trials were presented before each test. The mean number of trials in each PVT administration was 57. Outcome measures reported here are the number of lapses in attention (quantified as RTs ≥ 500 ms), overall mean RT, intra-individual RTV (quantified as the standard deviation (SD) in RTs[63]), and optimum response capability (quantified as the mean of the 10% fastest RTs).

Covariates

Chronotype was assessed with a reduced version of the Horne & Östberg Morningness-Eveningness Questionnaire (r-MEQ)[64]. The r-MEQ has five questions probing individuals' circadian preferences, yielding a total score ranging from 4 to 25. A score of 4-7 = 'Definitely Evening Type', 8-11 = 'Moderately Evening Type', 12-17 = 'Intermediate Type', 18-21 = 'Moderately Morning Type', and 22-25 = 'Definitely Morning Type'. 'Definitely evening type' and 'definitely morning type' is often referred to as "extreme" chronotypes.

Season was not systematically manipulated between nor within subjects (each subject underwent laboratory testing in one season only, across a study period of three weeks) but was entered as a covariate in statistical analyses. As there is substantial variation in annual photoperiod length at northern latitudes[65], all four seasons were included as categorical levels. December-February represented 'winter', March-May represented 'spring', June-August represented 'summer', and September-November represented 'fall'.

Sleep efficiency the night preceding each test session was derived from wrist actigraphy data, recorded in epochs of one minute duration. Threshold sensitivity was set to 'medium' (40 counts per minute) (Actiware version 6.0.9, Philips Respironics, Inc., United States). Rest intervals were scored based on i) the participants pushing an event button together with ii) raw data, and iii) information from sleep diaries. When the event button was not pushed, information from the two latter data sources were used. For each rest interval, sleep efficiency was calculated as total sleep time divided by interval duration minus total invalid time, multiplied by 100.

Statistical analyses

The analysis plan was also pre-registered at OSF, together with the hypotheses (https://osf.io/m7gfh). Missing data (< 10%) were imputed with a Random Forest algorithm in the R package *mice*[66]. All analyses were performed in R version 4.4.1[67] using the packages *tidyverse*[68], *glmmTMB*[69], *lme4*[70], *lmerTest*[71], *merDeriv*[72], *DHARMa*[73], *performance*[74], *parameters*[75], *emmeans*[76], and *effectsize*[77]. Data from the five practice trials on the PVT were

excluded from analyses. The distribution of residuals was evaluated with Q-Q plots, and model assumptions were checked. The number of lapses were analyzed with a Generalized Linear Mixed-Effects Model (GLMM) using a generalized Poisson distribution, as the number of lapses did not exhibit significant zero-inflation nor overdispersion. RTV was also analyzed with a GLMM due to right-skewness in the data. In the GLMMs, 95% Confidence Intervals (CIs) and p-values were computed using a Wald z-distribution approximation. Mean RT for all trials and the mean of the 10% fastest RTs were each analyzed with a Linear Mixed Effects-Model (LMM) using Restricted Maximum Likelihood (REML). In the LMMs, 95% CIs and p-values were computed using a Wald t-distribution approximation. As the residuals of RTV, mean RT, and mean 10% fastest RTs deviated slightly from a normal distribution, variables were log-transformed prior to analysis to increase normality and stabilize variance in the models. In all analyses on PVT variables, light*block, chronotype, season, and sleep efficiency were modeled as fixed effects, subject was modeled with random intercept. The two other within-subjects factors of light and block were modeled using complex random intercepts[78], as models with a maximum random-effects structure justified by the data did not converge[79]. In the analysis of RTV, mean RT was added as an additional predictor because the mean and SD of RTs are often correlated to some extent[80]. The following reference levels for the categorical predictors were used in the analyses: dim (light), 1 (block), fall (season), and intermediate type (chronotype). First, an initial model with the interaction term light*block and the other fixed effects and complex random intercepts specified above was tested. As the interpretation of significant simple effects that are part of one or more interaction terms is conditioned on the levels of each predictor in the interaction(s)[81], significant 'simple' effects of light and/or block in the initial model were modeled as main effects in a subsequent model. We also constructed two models with the interaction term light*chronotype in one model and light*season in another model, controlling for the other fixed effects, including block as main effect. Finally, we also explored sex differences on all PVT measures, as there are some indications that sex influences acute alerting responses[82]. In these analyses, light and biological sex were entered as fixed effects, using 'dim' and 'female', respectively, as reference levels, and subject was modeled with random intercept. Alpha level was set to .05 two-tailed in all analyses. For the GLMMs on the number of lapses, we report each estimate as Incidence Rate Ratio (IRR, the exponentiated model coefficient) as appropriate for count data, together with 95% CI, SE, z-value, and p-value. For the GLMMs on RTV, estimates in terms of exponentiated model coefficients (as the model provides estimates on the log-scale) together with 95% CI, SE, z-value, and p-value are reported. Partial r (r_p) is reported as theoretical effect size in the GLMMs. An $r_p < .3$ is considered a small effect, $< .5$ is considered moderate, and $\geq .5$ is considered a large effect[83]. In the LMMs, exponentiated model coefficients together with 95% CI and SE, t-value, and p-value are reported. Theoretical effect sizes in the LMMs include Cohen's partial f^2 as recommended by Lorah[84]. A Cohen's $f^2 \geq .02$ is considered a small effect, $\geq .15$ medium, and $\geq .35$ large [83]. All effect sizes were estimated using the test-statistic approximation method and the *effectsize* package[77]. Explained variance statistics for each model include Nakagawa's adjusted (conditional) R^2 for the total

model, Nakagawa's marginal R^2 for the combined influence of the fixed effects, and the adjusted Intra-class Correlation Coefficient (ICC) for the random effects[85]. In case of significant main and/or interaction effects, post-hoc analyses using Tukey's Honest Significant Difference (HSD) were used to control the Family-Wise Error Rate (FWER). In these post-hoc analyses, t-values and the degrees of freedom were computed using a Kenward-Roger approximation, and Estimated Marginal Means (EMMs) together with 95% CI, and corrected p-values are reported. An *a priori* power analysis was conducted in the larger study only, named *ENLIGHT*, consisting of several work packages (the current study being one of them), assuming three subgroups of participants (young, healthy adults; healthy seniors; seniors with mild dementia/mild cognitive impairment) and multiple non-hierarchical regression analyses (see the pre-registration of the *ENLIGHT* study at https://osf.io/6nbr9). Hence, this power analysis does not apply to the mixed model analyses in this study with a sample consisting of only one of the three subgroups and a hierarchical structure of both fixed and random effects.

Results

Descriptive statistics

40 healthy, young adults participated in the study. 42 out of a total of 480 observations were excluded from analyses due to measurement errors, resulting in a sample of 39 participants (mean age: 21.7, SD = 2.6, range: 18-28) and 438 observations (Table 1). Mean rMEQ score was 13.8 (SD = 3.3), corresponding to an 'intermediate' chronotype. On average, participants went to bed at 23:47 (SD = 01:14) and woke up at 06:41 (SD = 32 minutes), resulting in an average sleep duration of 372 minutes (~ 6.2 hours, SD = 69.8 minutes). Upon arrival at the laboratory at 08:00, participants had been awake for an average of one hour and 18 minutes (SD = 32.4 minutes). On the PVT, irrespective of light manipulation and measurement block, participants' median number of lapses were 1 (range: 0-16), mean overall RT was 308.40 ms (SD = 40.50 ms), mean intra-individual RTV was 75.31 ms (SD = 71.27 ms), and the mean of the 10% fastest RTs was 242.96 ms (SD = 21.79 ms). 64% of the study sample habitually consumed one or more caffeinated beverages on a normal day. As caffeine consumption can affect attention[86], we checked whether there were any significant differences in PVT performance among participants who habitually consumed caffeine vs. those who did not. GLMMs (lapses and intra-individual RTV) and LMMs (mean RT and 10% fastest RTs) with each PVT metric as outcome, controlling for whether participants habitually consumed caffeine or not ("Yes", "No", respectively) and with random intercepts for each subject, confirmed that caffeine consumption did not affect performance (number of lapses: p = .541, mean RT: p = .377, intra-individual RTV: p = .974, mean 10% fastest RTs: p = .140).

Total N (females)	39 (24)
Age [Mean±SD]	21.7±2.6
Caffeinated beverages [Median (range)]	1 (0-5)
Sleep efficiency [Mean±SD, %]	83.5±8.9
Chronotype N (%)	
Definitely morningness	0 (0)
Moderately morningness	7 (17.9)
Intermediate type	22 (56.4)
Moderately eveningness	10 (25.6)
Definitely eveningness	0 (0)
Season N (%)	
Spring	10 (25.6)
Summer	5 (12.8)
Fall	18 (46.2)
Winter	6 (15.4)
Laboratory conditions*	
Temperature [Mean±SD, °C]	20±1.2
Humidity [Mean±SD, %]	39.8±13.2

Table 1. Descriptive statistics of study sample and laboratory characteristics. Chronotype was assessed with a reduced version of the Morningness-Eveningness Questionnaire. There were no extreme chronotypes. Sleep efficiency was derived from wrist actigraphy. Caffeinated beverages represent the median number of caffeinated beverages (coffee, caffeinated tea, energy drink) habitually consumed on a normal day. *Kruskal-Wallis Rank Sum Tests did not reveal any significant differences in temperature nor air humidity between light conditions.

Acute alerting effects of light

Line plots of the progress in RTs from trial 1 to 54 in each light condition, stratified by measurement block, are provided in Supplementary Materials S3, Fig. S3.1.1-S3.1.3.

As the initial adjusted models with the interaction term light*block revealed significant simple effects of light and/or block but no significant interactions, light and block were modeled as separate fixed effects in subsequent main effects models. Results from these models are described below. Model estimates, effect sizes, and explained variance statistics are provided in Table 2 (GLMMs) and Table 3 (LMMs).

On all PVT measures except for RTV, participants responded slower over time (main effects of measurement blocks; p's < .001, see Supplementary Materials S3, Fig. S3.2.1, Fig. S3.3.1, Fig. S3.4.1, and Fig. S3.5.1). Additional figures from main-effects analyses can be accessed in Supplementary Materials S4 (Fig. S3.2.2 and Fig. S3.5.2). Sensitivity analyses on a dataset with complete-cases only showed a similar overall pattern of results (see Supplementary Materials S4, section S4.1-S4.4) as in analyses on imputed data, except for a significant main effect of light on RTV (larger variability in LWL compared to DL; $p_{corrected}$ = .031, Fig. S4.3.2), which did not appear in analyses on imputed data. However, this result should be interpreted with caution, as estimates are often biased in complete-case analyses when data is not missing completely at random. Additionally, we also constructed "crude" main-effects models unadjusted for the potential influence of chronotype, season, and sleep

efficiency, with light and block included as the only fixed effects and a CRI for each of the three random effects (subject, light, block). The effects of light and block in these analyses were similar to the results reported below. Model estimates from these "crude" models are provided in Supplementary Materials S5, Table S5.1-S5.4.

Lapses

The analysis of the number of lapses showed significant main effects of light (SWL: p = .004, r_p = -0.42; LWL: p = .002, r_p = -0.44; BWL: p = .044, r_p = -0.31, Table 2). Post-hoc analyses showed that participants had significantly fewer lapses in SWL (p = .023, *EMM* = 0.89[0.63-1.27], *SE* = 1.20) and LWL (p = .010, *EMM* = 0.85[0.59-1.22], *SE* = 1.20), compared to DL (*EMM* = 1.48[1.05-2.10], *SE* = 1.20) (Fig. 2).

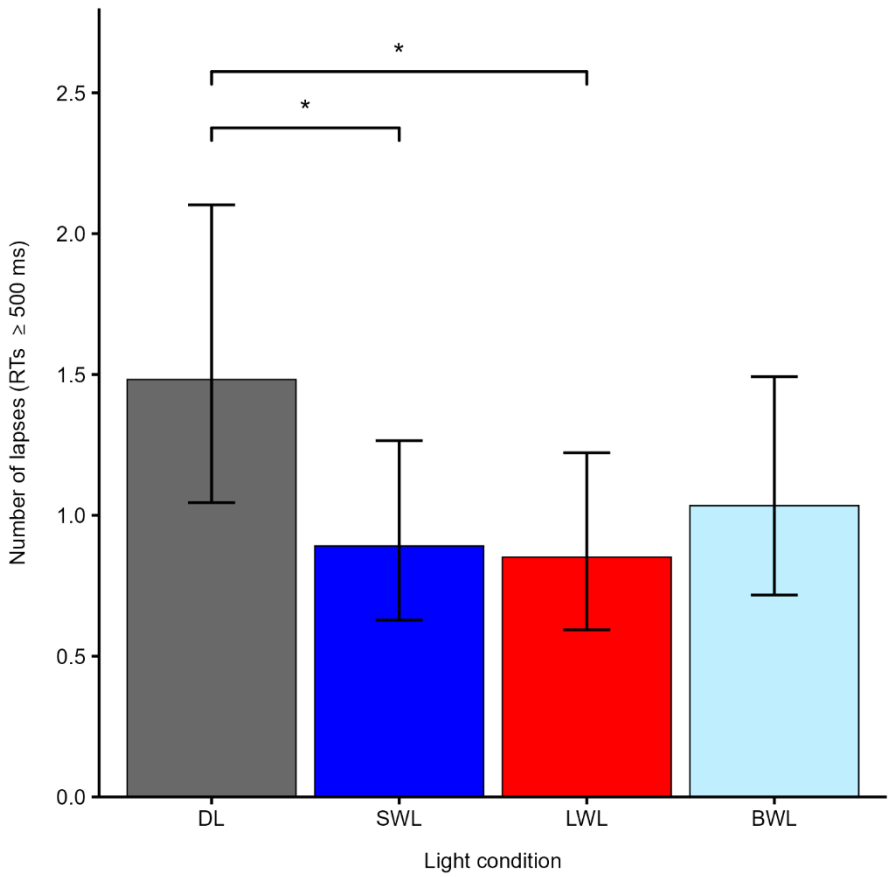

Figure 2. Estimated Marginal Means (EMMs) of the number of lapses in each light condition. Error bars = 95% Confidence Intervals (CIs). EMMs and CIs were back-transformed from log to original scale for visualization purposes. BWL = Bright White Light. DL = Dim Light. LWL = Long-Wavelength Light. ms = milliseconds. RTs = Reaction Times. SWL = Short-Wavelength Light. *p < .05.

There was also a significant main effect of season (spring vs. fall: p = .027, r_p = 0.33, Fig. S3.2.2), but the effect was no longer significant after correcting for multiple comparisons. Also, the model with the interaction term light*season revealed a significant interaction

between SWL and winter (p = .025), but this effect was also no longer significant after correcting for multiple comparisons. There were no significant light*chronotype interactions.

Mean RT

The main effects model showed significant main effects of light (SWL: p = .001, f^2 = 0.11; LWL: p = .004 f^2 = 0.09; BWL: p = .038 f^2 = 0.04). Post-hoc analyses revealed that participants' mean RT was faster in SWL (p = .008, *EMM* = 303.89[293.05-315.14], *SE* = 1.02) and LWL (p = .018, *EMM* = 305.12[294.20-316.45], *SE* = 1.02) compared to DL (*EMM* = 318.81[307.05-331.02], *SE* = 1.02, Fig. 3). Exploratory analyses showed no significant interactions between light and season nor between light and chronotype.

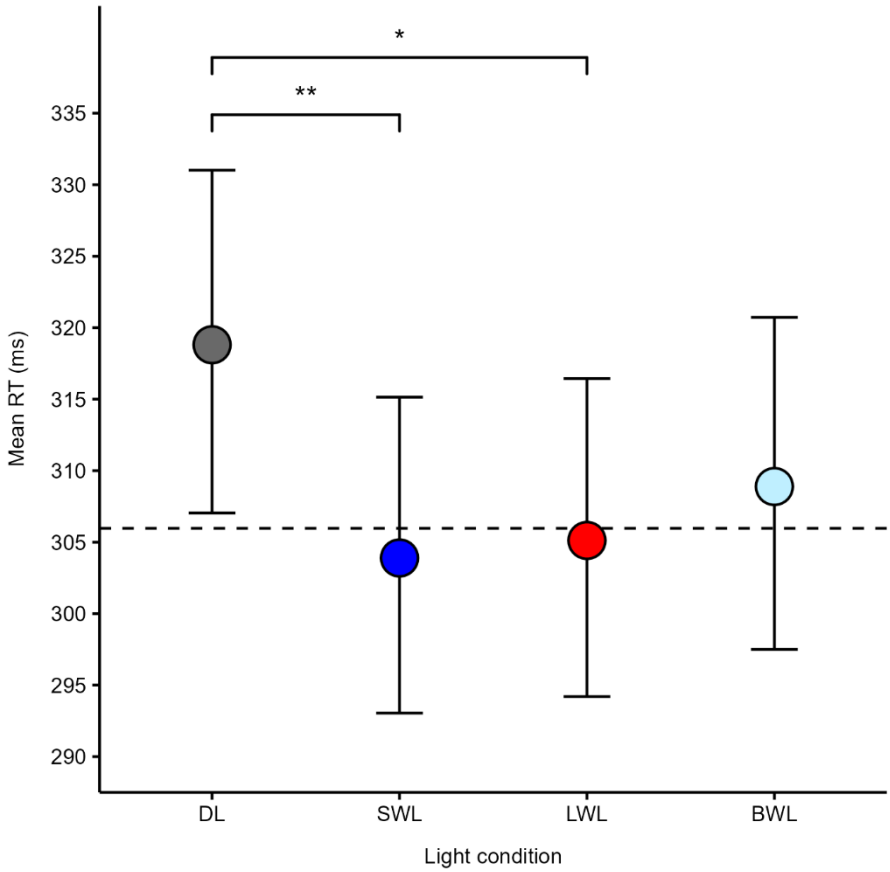

Figure 3. Estimated Marginal Means (EMMs) of Mean Reaction Time (RT) in each light condition. The y axis limit has been adjusted so that group differences appear more clearly. Error bars = 95% Confidence Intervals (CIs). Dashed line represents mean estimated RT across SWL, LWL, and BWL. EMMs and CIs were back-transformed from log to original scale for visualization purposes. BWL = Bright White Light. DL = Dim Light. LWL = Long-Wavelength Light. ms = milliseconds. SWL = Short-Wavelength Light. **p < .01. *p < .05.

RTV

The main effects model showed a significant main effect of mean RT ($p < .0001$, $r_p = 0.943$), in that variability in RT increased with longer RTs ($p < .001$, Spearman's $\rho = .70$ [95% CI: .65-.75], Fig. 4).

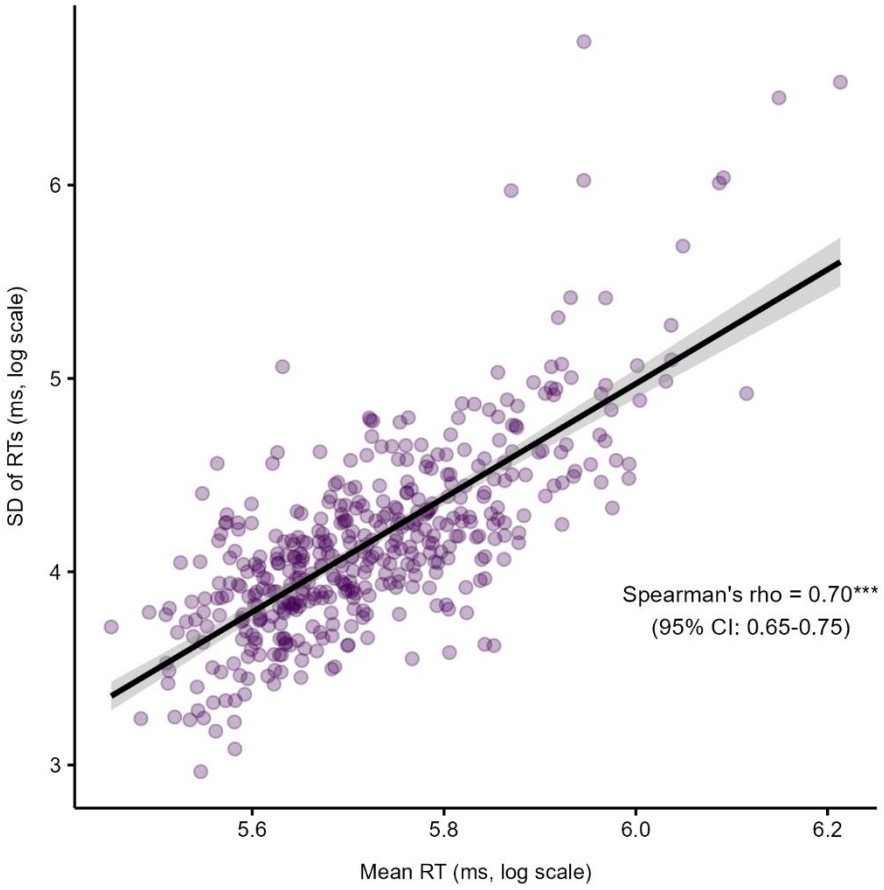

Figure 4. Scatter plot of the relationship between standard deviations in reaction time (RT) and mean RT. Values are on log scale. Error band = 95% Confidence Interval (CI). ms = milliseconds. ***$p < .001$.

There were also significant main effects of measurement blocks (block 1: $p < .001$, $r_p = -0.51$; block 2: $p < .001$, $r_p = -0.61$, Table 2). Post-hoc analyses showed that participants expressed lower variability in block 2 ($p < .001$, *EMM* = 60.61[55.76-65.88], *SE* = 1.04) and 3 ($p < .0001$, *EMM* = 58.03[53.30-63.18], *SE* = 1.04), relative to block 1 (*EMM* = 69.70[64.04-75.87], *SE* = 1.04), see Supplementary Materials S2. There were no significant main effects of light, season, and chronotype, and no significant interactions.

Mean of the 10% fastest RTs

The main effects model on the mean of the 10% fastest RTs showed significant main effects of light (SWL: $p = .017$, $f^2 = 0.06$; LWL: $p = .005$, $f^2 = 0.08$), chronotype (eveningness: $p = .019$, $f^2 = 0.03$; morningness: $p = .023$, $f^2 = 0.02$), and season (summer: $p = .018$, $f^2 = 0.16$), see Table

3. Post-hoc analyses showed that participants responded faster in LWL (p = .030, *EMM* = 243.11[236.88-249.51], *SE* = 1.01) compared to DL (*EMM* = 248.57[242.08-255.24], *SE* = 1.01), see Fig. 5. Post-hoc analyses on the main effect of season showed that participants tested in winter responded faster (p = .048, *EMM* = 234.68[222.32-247.73], *SE* = 1.03) than participants tested in summer (*EMM* = 261.25[246.19-277.23], *SE* = 1.03, Fig. S3.5.2). Post-hoc analyses of the main effects of chronotype did not remain significant after correction for multiple comparisons, and the interaction models of light*season and light*chronotype showed no significant interactions.

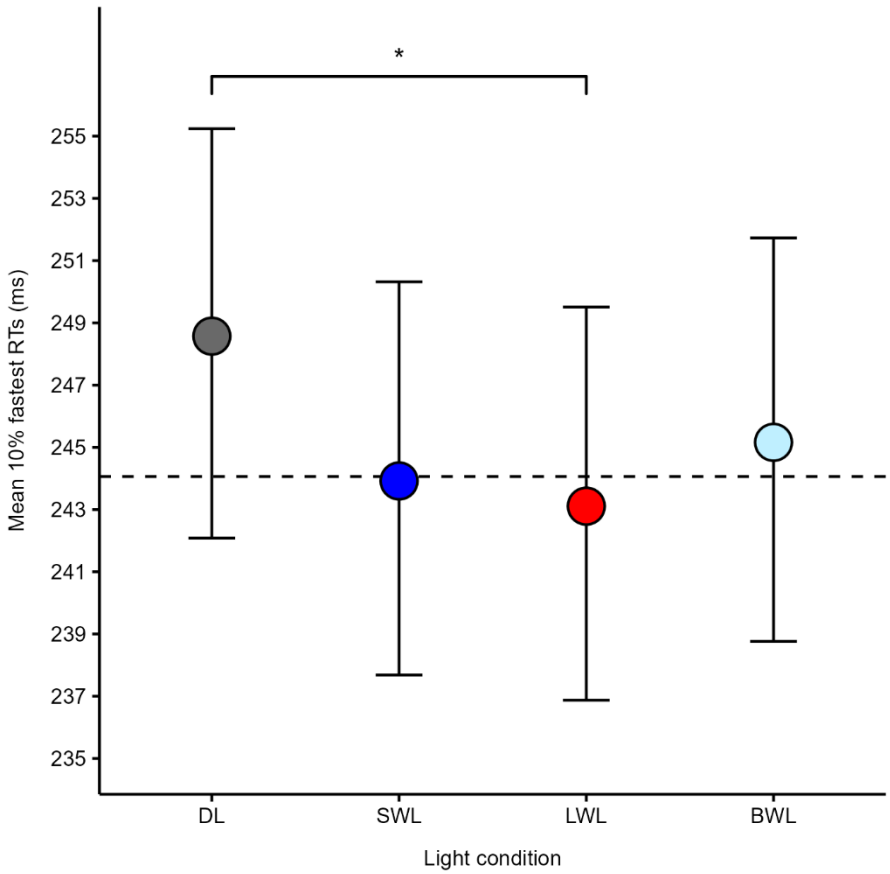

Figure 5. Estimated Marginal Means (EMMs) of the Mean 10% fastest Reaction Times (RTs). The y axis limit has been adjusted so that group differences appear more clearly. Error bars = 95% Confidence Intervals (CIs). Dashed line represents mean estimated 10% fastest RT across SWL, LWL, and BWL. EMMs and CIs were back-transformed from log to original scale for visualization purposes. BWL = Bright White Light. DL = Dim Light. LWL = Long-Wavelength Light. ms = milliseconds. SWL = Short-Wavelength Light. *p < .05.

	Lapses					RTV				
Parameters	*IRR (95% CI)*	*SE*	*z*	*p*	r_p	*Coefficient (95% CI)*	*SE*	*z*	*p*	r_p
Intercept	1.04 (0.19 – 5.68)	0.90	0.50	0.562		2.04e-8 (0.00 - 0.00)	2.40E-08	-17.67	< .001	
Light										
SWL	0.60 (0.42 – 0.85)	0.11	-2.87	**.004**	-0.42	1.07 (0.99 - 1.16)	0.04	1.75	.081	0.27
LWL	0.57 (0.40 – 0.82)	0.10	-3.10	**.002**	-0.44	1.07 (0.99 - 1.15)	0.04	1.63	.104	0.25
BWL	0.70 (0.49 – 0.99)	0.12	-2.01	**.044**	-0.31	1.03 (0.95 - 1.11)	0.04	0.75	.452	0.12
Block										
Block 2	2.41 (1.82 – 3.19)	0.34	6.18	**< .001**	0.70	0.87 (0.81 - 0.93)	0.03	-3.75	**< .001**	-0.51
Block 3	2.48 (1.89 – 3.26)	0.35	6.50	**< .001**	0.72	0.83 (0.78 - 0.89)	0.03	-4.79	**< .001**	-0.61
Chronotype										
Eveningness	1.09 (0.68 – 1.75)	0.26	0.37	.714	0.06	0.94 (0.83 - 1.06)	0.06	-1.19	.235	-0.19
Morningness	1.07 (0.60 – 1.91)	0.32	0.22	.830	0.04	0.92 (0.79 - 1.06)	0.07	-1.19	.234	-0.19
Season										
Spring	1.92 (1.08 – 3.44)	0.57	2.21	**.027**	0.33	1.08 (0.92 - 1.26)	0.09	0.87	.384	0.14
Summer	1.38 (0.68 – 2.81)	0.50	0.89	.373	0.14	0.84 (0.69 - 1.03)	0.09	-1.71	.087	-0.26
Winter	0.97 (0.97 – 1.01)	0.35	-0.08	.934	-0.01	1.09 (0.91 - 1.31)	0.10	0.96	.338	0.15
Sleep efficiency	0.99 (0.97 - 1.01)	0.01	-0.64	.519	-0.10	1.00 (0.99 - 1.00)	2.42e-03	-1.14	.253	-0.18
Mean RT						46.99 (33.79 - 65.35)	8.24	22.76	**< .001**	0.96
Random effects	*Coefficient*					*Coefficient*				
SD (Residual)	1.29					0.26				
SD (Intercept: Subject)	0.56					0.17				
SD (Intercept: Subject:Light)	0.47					0.08				
SD (Intercept: Subject:Block)	0.22					0.08				
Adjusted / Unadjusted ICC	0.396 / 0.330					0.381 / 0.130				
Conditional / Marginal R^2	0.497 / 0.168					0.789 / 0.660				

Table 2. Generalized Linear Mixed-Effects Model analyses of the number of lapses and intra-individual reaction time variability on the Psychomotor Vigilance Task. Incidence Rate Ratio (IRR) values for lapses represent the exponentiated model coefficients. The coefficients in the model of RTV are also exponentiated, as the model provides estimates on the log-scale. Significant *p*-values are highlighted in bold. BWL = Bright White Light. CI = Confidence Interval. ICC = Intra-Class Correlation Coefficient. LWL = Long-Wavelength Light. RTV = Reaction Time Variability. SD = Standard Deviation. SE = Standard Error. SWL = Short-Wavelength Light.

	Mean RT					Mean 10% fastest RTs				
Parameters	*Coefficient (95% CI)*	*SE*	*t*(422)	*p*	f^2	*Coefficient (95% CI)*	*SE*	*t*(422)	*p*	f^2
Intercept	291.97 (250.83 – 339.85)	22.56	73.47	< .001		241.40 (220.52 - 264.27)	11.11	119.17	< .001	
Light										
SWL	0.95 (0.93 - 0.98)	0.01	-3.27	**.001**	0.11	0.98 (0.97 - 1.00)	7.76e-03	-2.39	**.017**	0.06
LWL	0.96 (0.93 - 0.99)	0.01	-2.99	**.003**	0.09	0.98 (0.96 - 0.99)	7.75e-03	-2.81	**.005**	0.08
BWL	0.97 (0.94 – 1.00)	0.01	-2.10	**.036**	0.04	0.99 (0.97 - 1.00)	7.98e-03	-1.71	.088	0.03
Block										
Block 2	1.08 (1.06 - 1.10)	9.20e-03	9.10	**< .001**	1.10	1.04 (1.03 - 1.05)	6.68e-03	6.16	**< .001**	0.51
Block 3	1.10 (1.08 - 1.12)	9.34e-03	10.95	**< .001**	1.60	1.05 (1.03 - 1.06)	6.71e-03	7.12	**< .001**	0.68
Chronotype										
Eveningness	1.02 (0.97 - 1.06)	0.02	0.75	.452	e.78e-03	1.04 (1.01 - 1.07)	0.02	2.35	**.019**	0.03
Morningness	1.01 (0.96 - 1.06)	0.03	0.30	.764	5.44e-04	1.04 (1.01 - 1.08)	0.02	2.29	**.023**	0.02
Season										
Spring	1.04 (0.97 - 1.12)	0.04	1.24	.285	0.04	1.01 (0.96 - 1.06)	0.03	0.42	0.676	4.82e-03
Summer	1.09 (1.00 - 1.19)	0.05	1.92	.064	0.11	1.08 (1.01 - 1.16)	0.04	2.37	**.018**	0.16
Winter	0.99 (0.91 - 1.07)	0.04	-0.30	.732	2.73e-03	0.97 (0.92 - 1.03)	0.03	-0.93	.355	0.03
Sleep Efficiency	1.00 (1.00 - 1.00)	0.00	-0.09	.363	4.24e-05	1.00 (1.00 - 1.00)	4.99e-04	-0.96	.337	5.76e-03
Random Effects	*Coefficient*					*Coefficient*				
SD (Residual)	0.07					0.05				
SD (Intercept: Subject)	0.08					0.06				
SD (Intercept: Subject:Light)	0.05					0.02				
SD (Intercept: Subject:Block)	8.70e-03					0.02				
Adjusted / Unadjusted ICC	0.633 / 0.516					0.685 / 0.534				
Conditional / Marginal R^2	0.701 / 0.185					0.754 / 0.220				

Table 3. Linear Mixed-Effects Model analyses of mean reaction time and the mean of the 10% fastest reaction times on the Psychomotor Vigilance Task. Significant p-values are highlighted in bold. Model coefficients are exponentiated, as the models provide coefficients on the log-scale. BWL = Bright White Light. CI = Confidence Interval. ICC = Intra-Class Correlation Coefficient. LWL = Long-Wavelength Light. RT = Reaction Time. SD = Standard Deviation. SE = Standard Error. SWL = Short-Wavelength Light.

Discussion

This study tested whether daytime exposure to artificial light conditions of high and low melanopic illuminance, against a control condition of white DL (< 10 melanopic lux), could enhance alertness and attention in healthy, young adults. In addition to commonly reported central tendency measures from the PVT (lapses, mean RT, and mean 10% fastest RTs), this study reports for the first time, results on the acute alerting impact of light on intra-individual RTV. Overall, the results partly supported our main hypothesis, showing that narrow bandwidth SWL and LWL, compared to the DL control condition, reduced lapses and shortened overall mean RT. Light did not exert acute effects on RTV. Surprisingly, there were no significant effects of BWL on either of the PVT measures, despite that the BWL condition was also of relatively high melanopic illuminance. And, contrary to our explorative hypothesis, we did not find evidence supporting that SWL was superior to LWL. Hence, irrespective of melanopic illuminance level, both SWL and LWL induced acute alerting effects.

The light exposure duration and illuminance levels in our study differs from other studies in the field. Hence, a direct comparison of results across studies is challenging, especially when previous studies do not include information on the m-EDI of the light conditions. Additionally, relatively few prior studies have assessed PVT performance during or immediately following exposure to narrow bandwidth lights during daytime[44,49,54], limiting the comparison of the current results to findings from other studies. Nevertheless, our finding of an acute alerting effect of SWL, compared to DL, on lapses and mean RT are in line with findings from Rahman et al.[87], although this study used medium-wavelength "green" light rather than DL as control condition, and the duration of SWL was considerably longer; 6.5 hours. Another study, by Laszewska et al.[30], showed that 40 minutes of exposure to SWL in the early afternoon reduced EEG markers of drowsiness/sleepiness[30]. Hence, it appears that SWL of different exposure durations can exert positive effects on various indicators of alertness during daytime. However, this might apply to continuous light exposure patterns only. In a study using intermittent light exposure in 5-minute light intervals separated by varying periods of darkness, there was no significant effect of SWL on lapses and mean RT[54].

In the evening and during nighttime, acute alerting effects of SWL in humans have been linked to mechanisms involving the suppression of melatonin[13,88], a neurohormone involved in the biological timing of sleep[89]. In young adults, the spectral sensitivity of melatonin suppression lies close to the spectral sensitivity of ipRGCs/melanopsin[90]. It has therefore been hypothesized and also demonstrated that light which theoretically activates melanopsin to a large extent is a strong predictor of light's alerting effects during times-of-day where circadian clocks promote sleepiness and relaxation[91]. However, it should be noted that, even though light of high m-EDI prior to bedtime can suppress melatonin by ~ 14% compared to low m-EDI light, behavioral and self-report measures of sleepiness and alertness are not necessarily affected depending on high vs. low m-EDI[92]. Notably, it has been shown that also LWL of low m-EDI can suppress nighttime melatonin levels[93]. Hence, the mechanistic effects

underlying the alerting effects of light during nighttime cannot be entirely attributed to melatonin suppression alone. During daytime, when the circadian clock promotes wakefulness and there is hardly any melatonin present in the human body[89], other mechanistic explanations are needed to account for light's alerting effects. One plausible mechanism underlying the alerting potential of SWL during daytime is likely associated with light-induced brain activity in areas comprising the alerting network. The alerting network, one of the brain's main attention networks[94], consists of several frontal and parietal areas including the dorsolateral prefrontal cortex (DLPFC) and the anterior cingulate cortex (ACC), as well as the Locus Coeruleus (LC) in the brain stem. During or immediately following exposure to SWL, studies using functional Magnetic Resonance Imaging (fMRI) have shown activations in the DLPFC, the ACC, and an area in the brain stem compatible with the LC[95,96]. Moreover, stable performance on the PVT has been linked to greater functional connectivity between the DLPFC and other cortical areas[49]. However, to date, only one study has tested the impact of SWL on the efficiency of the alerting network, measured using the RT-based Attention Network Test (ANT)[97]. This study reported no significant effect of SWL[98], however, the light exposure duration was rather brief (5 minutes). Hence, it is possible that longer exposure durations such as e.g., 30 minutes as in the fMRI study by Alkozei et al.[96] are needed to enhance alertness during daytime. Meanwhile, an fMRI study by Vandewalle et al.[95] showed that 50 seconds of SWL was sufficient to induce activations in brain areas associated with the alerting network. The differences in observed effects of various exposure durations of SWL are likely associated with the large heterogeneity across studies when it comes to illuminance levels, the specific time-of-day, individual differences in light sensitivity, and direct and indirect influences of circadian phase and sleep on alertness. Also, it should be noted that these fMRI studies examined brain responses to light in association with a working memory task probing executive processes more than alertness *per se*. No study has yet tested the effect of SWL on the alerting network in terms of ANT performance assessed simultaneously with fMRI. It therefore remains unknown whether SWL modulates the alerting network at a neurophysiological level sufficient to affect alertness at the behavioral level.

Beyond acute alerting effects of SWL on lapses and mean RT, we also observed similar acute alerting responses during exposure to LWL, including a positive effect on the most optimum responses (10% fastest RTs). However, other studies report no significant effects of LWL on mean RT on the PVT[31,54]. Although the light exposure duration and control light condition in the study by Sahin et al.[31] were comparable to those in our study, a direct comparison of findings are still somewhat challenging though, as the study used a task probing alertness over a longer time period (i.e., sustained attention) and the illuminance level were much lower (213 vs. ~ 560 photopic lx in our study). The absence of a significant effect of LWL on mean RT on the PVT was also reported in one of the experiments in van der Meijden et al.[54] However, again, results cannot be directly compared as this study used an intermittent light exposure pattern which differs from our continuous exposure. Also, the illuminance level of LWL in van der Meijden et al.[54] was only 40 photopic lx, which might not be sufficient to induce alerting responses during the day. When it comes to other PVT

521 measures, our study is the first to test the acute daytime effects of LWL on lapses and the
522 mean 10% fastest RTs. Hence, future studies are needed to confirm our findings.
523 Nevertheless, acute alerting effects of LWL during the day, with exposure durations ranging
524 from 40 to 110 minutes, have been observed in studies that have assessed the effects on
525 neurophysiological indicators of alertness/drowsiness, such as EEG alpha power[11,30,31].
526 However, null findings have also been reported[59]. Additionally, it has been shown that LWL
527 disrupts brain regions associated with goal-oriented behavior[99], and that "orange" light (λ_{max}
528 = 590 nm) does not modulate the connectivity between a subcortical and cortical brain
529 region involved in regulating attention[100]. Though, one should keep in mind that i) neither of
530 these two fMRI studies investigated brain responses to tasks probing alertness *per se*, ii) nor
531 did the studies test the efficiency of the alerting network, and iii) the duration of light
532 exposure was brief (60 and 30 seconds, respectively). Hence, the impact of LWL on alertness
533 and attention remains rather inconclusive in the literature depending on the methodology,
534 including the quantification of alertness, and it remains to be tested whether LWL can
535 activate brain regions in the alerting network in a similar extent to activations associated with
536 exposure SWL[95,96].

537 Melanopic illuminance has been shown to predict various NIF responses to light[91]. The
538 SWL condition used in our study was of considerably high melanopic illuminance (~ 1400 lx)
539 whereas the LWL condition had a low melanopic illuminance (< 5 lx). We therefore
540 hypothesized that SWL would be superior to LWL in inducing alerting effects in our sample.
541 However, the results contradicted this hypothesis as there were no differential effects of SWL
542 relative to LWL on any of the PVT measures. Killgore et al.[49] reported similar findings of no
543 significant differences in lapses were found following 30 minutes of SWL versus LWL in the
544 late morning. One possible explanation for no significant differences between SWL and LWL
545 in our study might be that the two narrow bandwidth lights were matched on photon
546 irradiance. When aiming at designing a SWL light condition with a m-EDI > 1000 lx, matching
547 SWL and LWL on photon irradiance or photon flux results in relatively high L-cone-opic
548 irradiance and photopic illuminance of LWL. Since melanopsin and other retinal
549 photopigments follow the 'principle of univariance', stating that the output of a given
550 photoreceptor is dependent on the total amount of photons absorbed, high-intensity LWL
551 has the potential to induce alerting responses as the photoreceptors does not distinguish
552 between differences in wavelength vs. intensity[19,101]. It has been proposed that LWL can
553 modulate NIF responses through synaptic inputs from L-cones to the ipRGCs[102]. However, as
554 retinal photoreceptors have distinct yet overlapping spectral sensitivities, a light condition
555 which peaks at e.g., 625 nm (corresponding to "red" LWL) will stimulate not only L-cones but
556 the other photoreceptors as well. To be able to conclude mechanistically on the distinct
557 photoreceptor contributions to NIF responses, metameric light conditions obtained through
558 the method of 'silent substitution' are needed[103]. Metameric lights are pairs of light
559 conditions that appear visually similar to an observer but differ in their relative stimulation of
560 the different photoreceptors[104]. By applying this methodology, it has recently been concluded
561 that there is a lack of strong evidence to support the idea that cones contribute to circadian

562 and alerting responses[105]. In this study, alertness was measured using self-report and the
563 authors used flickering lights at night. It therefore remains to be seen whether the conclusion
564 from this paper also holds when light exposure is delivered during daytime and alertness is
565 measured using performance tasks and/or neurophysiological methods.

566 Contrary to one of our main hypotheses, BWL did not induce significant alerting effects
567 despite being of relatively high melanopic illuminance (~ 1000 melanopic lx) and CCT (~ 8000
568 K). This finding contrasts results from two other studies testing the effects of BWL or short-
569 wavelength-enriched white light at a similar time-of-day as that in our study[45,55].
570 Nevertheless, as shown in a recent systematic review by our lab[27], most studies report no
571 significant effects of BWL and short-wavelength-enriched white light on PVT measures. It is,
572 however, unclear which parameters of BWL are the most effective in inducing alerting
573 responses during the day. Although it has been recommended that daytime light should
574 measure at least 250 melanopic lx at eye level[106], dose-response curves for the acute alerting
575 effects of light during daytime have not yet been firmly established. E.g., Smolders et al.[107]
576 did not find evidence of any clear dose-response relationships between 1h of exposure to
577 white light (intensity range: ~ 14-1000 melanopic lx) during daytime on alertness. Irrespective
578 of the specific light spectrum, dose-response curves for alerting responses to light will
579 depend not only on exposure duration, but probably also on the specific time-of-day of
580 exposure, e.g., morning versus afternoon. In the afternoon, following lunch, some people
581 experience a dip in core body temperature (i.e., the "post-lunch dip"), which can have
582 negative impacts on performance on cognitive tasks[108]. It is possible that we might have
583 observed alerting effects of BWL with an exposure duration extending into the post-lunch
584 dip[56,109]. Furthermore, the duration of light adaptation was 30 minutes in our study. This
585 duration is similar to other studies in the field, and it aligns with neurophysiological
586 responses to light, showing that the half-maximum EEG gamma response (associated with
587 cognitive processes and attention) is achieved after approx. 12 minutes of light exposure[110].
588 Still, it might be shown in future studies that a longer light adaptation than 30 minutes prior
589 to cognitive testing might be needed for polychromatic BWL to induce improvements in
590 alertness and cognitive functioning during the day.

591 Irrespective of light manipulations, prolonged time in testing or repeated test
592 administrations might result in so-called time-on-task effects. On the PVT, this manifests as
593 increasingly slower RTs across administrations[111]. We found evidence of a time-on-task effect
594 on all PVT metrics except for RTV. Specifically, on the number of lapses, overall mean RT and
595 the mean 10% fastest RTs, there were significant main effects of measurement blocks with
596 slower RTs and more lapses from block 1 to 2, and from block 1 to 3. In between PVT blocks,
597 participants performed a series of other cognitive and emotion processing tasks, likely
598 contributing to increased fatigue across time. Apart from assessing main effects of
599 measurement blocks, we also examined whether exposure to light could counteract these
600 time-on-task effects, however, there were no significant interactions between light and

601 measurement block. This finding is consistent with results from previous studies[45,48,52],
602 although significant interactions have been reported as well[12,46].

603 Light exposure can not only affect alertness directly, in terms of acute effects, but also
604 indirectly by modulating circadian rhythms and sleep[112,113]. Melanopsin-containing ipRGCs
605 project to the "master" circadian clock, the SupraChiasmatic Nucleus (SCN) of the
606 hypothalamus. The SCN further projects to nuclei involved in regulating melatonin secretion,
607 sleep-related processes and alertness/arousal through a pathway connecting the SCN, the
608 dorsomedial hypothalamic nucleus and the LC[114]. Based on photic information from the
609 ambient light-dark cycle and information from other 'Zeitgebers' such as social activities and
610 meal consumption, the SCN entrains a host of circadian (~ 24 hour) rhythms throughout the
611 brain and body. One especially prominent role of ipRGCs when it comes to circadian rhythms
612 is phase shifting of the biological clock[115,116]. Depending on the timing of light exposure
613 relative to the trough of the core body temperature (CBT), light can either phase-advance the
614 clock if light exposure occurs in the morning (after the CBT trough), or phase-delay the clock
615 if light exposure occurs in the evening or at night (before the trough in CBT). Here, it has
616 been suggested that melanopic illuminance is the best predictor of light's effect on circadian
617 phase shifting[91]. The presentation order of the light conditions in our study was randomized
618 and counter-balanced within participants to limit confounding effects related to stronger
619 circadian entrainment following high m-EDI light (SWL and BWL) compared to low m-EDI
620 light (LWL and DL). However, we did not impose any control over participants' light exposure
621 in the evenings. It is therefore a possibility that artificial light emitted from short-wavelength-
622 enriched LED displays (e.g., from smartphones, tablets, and laptops) or other LED sources in
623 the evening had a phase-delaying effect on participants' circadian clock, and/or disrupted
624 their sleep[117], contributing to amplified alerting responses to light the subsequent days.
625 Furthermore, we did not control participants' light exposure behaviors the days in between
626 test sessions. As such, large inter-individual variations in light exposure behaviors during the
627 waking day (e.g., the amount of daylight received outdoors) can have acted as a confounder
628 in terms of effects on circadian phase entrainment, sleep, and altered light sensitivity.

629 Interindividual differences in light sensitivity also depend on seasonal variations in the
630 amount of solar light present in the environment; the length of the photoperiod. With shorter
631 photoperiods in the fall and winter – particularly at high latitudes – light sensitivity is
632 increased[41,118], thus potentially enhancing alerting responses to light. Indeed, we found that
633 participants tested in the fall had fewer lapses than participants tested in spring, and that
634 participants tested in winter had faster optimum responses (10% fastest RTs) than participants
635 tested in summer. However, we found no significant interactions between light and season,
636 hence, we cannot conclude on whether particular light conditions would be more optimal
637 than others for different seasons of the year. Also, as participants were tested in one season
638 only and the number of participants tested in each season was rather small and unbalanced
639 in groups, future research should be conducted with large enough sample sizes enabling the

manipulation of season between-subjects or with enough resources enabling repeated testing of the same individual across all four seasons of the year.

Alertness is regulated by circadian rhythms both directly in terms of the promotion of wakefulness and alertness at certain times of day, and indirectly, though circadian effects on sleep[119]. The direct effects of circadian rhythmicity on alertness manifest as reduced alertness upon awakening, rather stable levels throughout the day and reduced alertness again in the evening and at night[24]. Participants in our study were tested at a time-of-day where alertness levels are typically stable in well-rested individuals, promoting adequate cognitive performance on various tasks. However, certain study sample characteristics in the current study might have contributed to confounding effects to the observed results on light's acute effects on alertness. The sample in our study consisted mainly of university students. At a group level, studies indicate that university and college students report sleep difficulties and irregular bed and wake times[120–123]. Besides the potential confounding role of circadian phase shifting discussed above, mild acute sleep restriction might have acted as a confounding variable in our study. When sleep is restricted to a duration below an individual's optimal time in bed, daytime cognitive functioning is impaired, manifesting as e.g., lapses of attention[124]. Though we instructed participants to maintain regular bed and wake times throughout the study, we did not impose any requirements related to spending a certain amount of time in bed each night. As participants' sleep duration averaged over the four nights preceding each test session was 6.2±1.2 hours, some of the participants were likely mildly sleep deprived upon arrival at the laboratory, making them more sensitive to alerting effects of light. Furthermore, sleep deprivation can increase the severity of sleep inertia in the morning[125]. Sleep inertia is a state of reduced arousal and cognitive functioning immediately following awakening from sleep, which can reduce alertness over the course of a few minutes for up to as long as 3 hours, even in individuals that are not sleep deprived and went to bed at their habitual time[125]. Sleep inertia is further dependent on various factors, including prior sleep duration and the specific sleep stage preceding awakening from sleep[126]. Research have also shown that the effects of morning sleep inertia can depend on cognitive domain, with alertness being more negatively affected by sleep inertia than working memory[127]. In our sample, participants had been awake for an average of 78±32 minutes before entering the laboratory in the morning. Hence, some participants might have been suffering from sleep inertia at the time of testing, thereby likely benefitting more from exposure to light at this specific time-of-day. Additionally, the cognitive impairments associated with sleep inertia may have been worse for participants with a later circadian timing[128]. Later circadian phase has been identified in those who correspond to an 'evening' chronotype[129]. There were no extreme evening chronotypes (as measured with r-MEQ) in our sample, however, 25.6% reported a circadian preference corresponding to a 'moderately evening' chronotype. We looked at potential effects of chronotype on performance and in interaction with light but found no significant effects. However, the relatively low sample size in our study can have limited the detection of true null findings.

In sum, although findings in our study might have been confounded by the effects of sleep restriction and sleep inertia on cognitive functioning, a study sample consisting of a proportion of acutely, mildly sleep deprived university students is likely more representative of a "typical" larger population of college/university students, increasing ecological validity and generalizability.

To our knowledge, the current study is the first to test whether light influences intra-individual variability in RTs (RTV) as indexed by the SD in RTs[63]. RTV reflects fluctuations in attention and has been proposed as a neurophysiological marker of attentional lapses[130]. Therefore, one could expect similar acute alerting effects of light on RTV as on lapses. However, our results did not support this expectation, as there were no significant main effects of light on RTV. Instead, a large proportion of the variance in RTV could be explained by mean RT in our model (Spearman's ρ = .70), with increasingly slower mean RT associated with increasingly higher variability. Additionally, unlike other PVT metrics, RTV did not deteriorate over time. Rather, variability decreased across assessments, indicative of a stable response pattern. This might be related to ceiling effects in our young, healthy sample (see e.g., MacDonald et al.[131] for a review of changes in RTV across the life span and in relation to brain disorders).

This study has several limitations. First, the analysis of RTV would likely have benefited from a different modeling technique than a (generalized) linear mixed model. Often, RT distributions exhibit substantial right-skewness. Indeed, the residuals of RTV in our study were right-skewed. To better capture this skewness and the "pure" variability component of RTs, ex-Gaussian modeling might have been preferable. In an ex-Gaussian model, the RT distribution is separated into two gaussian and one exponential component, addressing some limitations of global measures such as the SD[63,130,132]. Unfortunately, we did not have enough PVT trials to reliably estimate the exponential component. Second, to be able to conclude on ipRGC/melanopsin-mediated acute alerting responses to light, metameric light conditions should have been used. Unfortunately, the lighting set-up in our lab did not have this design option. As metameric lights appear visually similar, the use of such light conditions could also have ruled out potential placebo effects arising from participants' expectations about what light conditions would increase alertness. Still, it can be argued that positive and negative effects of light when it comes to health and sleep (e.g., getting enough daylight and avoiding the use of visual LED displays in the evening and at night) are more known in public discourse than the neurobehavioral effects of more "extreme" light conditions such as those of SWL and LWL in our study. Hence, it is unlikely that our results stem from placebo alone. Third, although most point estimates remained significant after correction for multiple comparisons, some confidence intervals were wide, indicating uncertainty in estimates. Also, the sample size and the number of predictors in the models likely reduced statistical power, and effect sizes for the significant main effects of light were small to moderate. However, these effect size indices should be interpreted cautiously, as they cannot be estimated reliably in multilevel models with random-effect variance

720 components[84]. This is especially relevant for the results reported in our study, as the statistical
721 models were constructed with multiple random-effect terms to account for all known sources
722 of random variance associated with repeated testing on the same subjects over time.

723

724 Conclusion

725 Our findings suggest that exposure to artificial light of both low and high melanopic
726 illuminance during daytime can enhance alertness and attention in healthy, young adults, by
727 reducing lapses and improving overall mean RT and optimum response capability. Notably,
728 light of high melanopic illuminance was not superior to light of low melanopic illuminance –
729 both SWL and LWL improved alertness and attention. This finding challenges the traditional
730 theoretical assumptions underlying the NIF effects of light and suggests that the relationship
731 between light and attention during daytime may be more complex than previously
732 understood. Surprisingly, despite having relatively high melanopic illuminance, BWL did not
733 increase alertness, and light exposure did not impact short-term intra-individual RTV.
734 However, future research with higher sample sizes should test whether intra-individual RTV,
735 analyzed with more optimal modeling techniques such as Ex-Gaussian modeling, is acutely
736 affected by exposure to light.

737

738 Data availability

739 Aggregated behavioral data is available from the corresponding author upon request.

740

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Figure legends

Figure 1. Overview of experimental design. From 09:30 to approximately 11:00, participants performed a series of neurobehavioral tests assessing alertness (Psychomotor Vigilance Task (PVT)), cognitive control (Eriksen Flanker Task (EFT)), working memory (n-back) and aspects of emotion processing (implicit and explicit emotion recognition and a Go/No-Go task with emotional stimuli). Results from the EFT, n-back. and emotion tasks will be reported in future publications. The presentation order of light conditions and the order of cognitive vs. emotion-related tests were randomized and cross-

balanced within groups of participants, however, not for the PVT, as this task was administered in three blocks at fixed intervals throughout light exposure (at ~ 09:40, ~ 10:15, and ~ 10:50).

Figure 2. Estimated Marginal Means (EMMs) of the number of lapses in each light condition. Error bars = 95% Confidence Intervals (CIs). EMMs and CIs were back-transformed from log to original scale for visualization purposes. BWL = Bright White Light. DL = Dim Light. LWL = Long-Wavelength Light. ms = milliseconds. RTs = Reaction Times. SWL = Short-Wavelength Light. *$p < .05$.

Figure 3. Estimated Marginal Means (EMMs) of Mean Reaction Time (RT) in each light condition. The y axis limit has been adjusted so that group differences appear more clearly. Error bars = 95% Confidence Intervals (CIs). Dashed line represents mean estimated RT across SWL, LWL, and BWL. EMMs and CIs were back-transformed from log to original scale for visualization purposes. BWL = Bright White Light. DL = Dim Light. LWL = Long-Wavelength Light. ms = milliseconds. SWL = Short-Wavelength Light. **$p < .01$. *$p < .05$.

Figure 4. Scatter plot of the relationship between standard deviations in reaction time (RT) and mean RT. Values are on log scale. Error band = 95% Confidence Interval (CI). ms = milliseconds. ***$p < .001$.

Figure 5. Estimated Marginal Means (EMMs) of the Mean 10% fastest Reaction Times (RTs). The y axis limit has been adjusted so that group differences appear more clearly. Error bars = 95% Confidence Intervals (CIs). Dashed line represents mean estimated 10% fastest RT across SWL, LWL, and BWL. EMMs and CIs were back-transformed from log to original scale for visualization purposes. BWL = Bright White Light. DL = Dim Light. LWL = Long-Wavelength Light. ms = milliseconds. SWL = Short-Wavelength Light. *$p < .05$.

Author contributions

Writing original draft, planning and conducting statistical analyses, preparing figures and tables: LBB. Methodology and conceptualization: EF-G, EV, IHN, LBB, LS. Funding acquisition: EF-G, IHN, LS. Recruitment of participants: LBB, OBK, MEH, EF-G, EV, IHN. Data collection: LBB, OBK, MEH. Reviewing draft and approving final manuscript for submission: all authors.

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Competing Interests

The authors declare no competing interests.