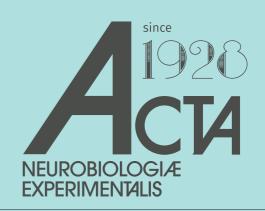
DOI: 10.21307/ane-2021-011



The influence of light exposure and chronotype on working memory in humans

Bartosz Kossowski^{1*}, Dawid Droździel¹, Katarzyna Rode^{1,2}, Jarosław Michałowski³, Konrad S. Jankowski², Marek Wypych¹, Agnieszka Wolska⁴ and Artur Marchewka^{1*}

Laboratory of Brain Imaging, Nencki Institute of Experimental Biology, Polish Academy of Science, Warsaw, Poland, ² Faculty of Psychology, University of Warsaw, Warsaw, Poland, ³ Poznan Laboratory of Affective Neuroscience, Department of Psychology and Law, SWPS University of Social Sciences and Humanities, Poznan, Poland, ⁴ Central Institute for Labour Protection, National Research Institute (CIOP-PIB), Warsaw, Poland, *Email: b.kossowski@nencki.edu.pl, a.marchewka@nencki.edu.pl

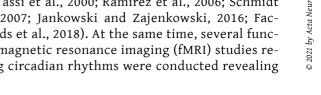
Here we examine how exposure to blue (peaking at λ =470 nm), green (peaking at λ =505 nm) and red (peaking at λ =630 nm) light affects subsequent working memory performance measured with visual N-back tasks and associated functional brain responses in participants with extreme morning and extreme evening chronotype. We used within-subjects experimental manipulation on carefully selected samples and state of the art equipment for light exposure. The results show no differences between extreme morning-type and evening-type individuals in N-back task performance. We also did not replicate the alerting effect of exposure to blue wavelength light, supposedly enhancing performance on cognitive tasks. However, we found higher brain activity in the morning hours for extreme morning in comparison to extreme evening chronotype in several frontal areas of the precentral gyrus, middle and superior frontal gyri and in the occipital gyrus. This may indicate increased strategic or attentional recruitment of prefrontal areas, implicated in compensating working memory load in the morning type.

Key words: chronotype, wavelength, light, fMRI, working memory

INTRODUCTION

There are several factors influencing our daily cognitive functioning and sleeping routines. For instance, our jobs and social networks could impact and change our day-to-day functioning. However, the strongest factor originates from homeostatic process and circadian rhythms that regulate sleep-wake behaviour (Borbély et al., 2016). The propensity of a person to be awake and to be asleep during a particular time over 24 h light-dark cycles is called a chronotype. Chronotypes were shown to be rather stable traits of the subjective diurnal rhythm of activity. They refer to the subjective morning vs. evening preferences and are measured with self-report tests providing information on the preferred hours for waking up and retiring to sleep, times of the day subjectively considered by a person as optimal for physical and intellectual performance, as well as the levels of arousal and well-being of the subject at different times throughout the day (Smith et al., 1989; Jankowski, 2015).

Time-of-day effects have been discovered in various cognitive tasks including attentional processes, working memory, as well as verbal and arithmetic tests (Tassi et al., 2000; Ramírez et al., 2006; Schmidt et al., 2007; Jankowski and Zajenkowski, 2016; Facer-Childs et al., 2018). At the same time, several functional magnetic resonance imaging (fMRI) studies regarding circadian rhythms were conducted revealing





alteration in brain activation patterns during night and afternoon hours (Gorfine and Zisapel, 2009) and group differences which depended on chronotype (Gorfine et al., 2007; Fafrowicz et al., 2009; Schmidt et al., 2009, 2012, 2015; Peres et al., 2011).

Light exposure is another important factor influencing physiology and cognition in humans and evokes non-visual effects, independent of visual perception. These non-visual effects include the regulation of circadian rhythms, melatonin production, changes in core body temperature, sleep propensity, and alertness. The existence of intrinsically photosensitive retinal ganglion cells (ipRGc) containing melanopsin make it feasible to capture the non-visual information of light and activate the circadian system (Berson et al., 2002). Several studies have suggested that the effect of blue light exposure is stronger than white light (Cajochen, 2007; Holzman 2010). This is explained by maximum sensitivity of ipRGc to short wavelength radiation between 460 and 480 nm (Dijk and Archer, 2009). A recent fMRI study has shown that blue light has a beneficial impact on working memory performance and elicits measurable functional brain responses within prefrontal regions associated with executive functions (Alkozei et al., 2016). However, it remains to be determined how different wavelengths of light influence behaviour and how brain response as a function of wavelength is modulated by person's chronotype.

The goal of the present study was to explore how exposure to blue (peaking at λ =470 nm), green (peaking at λ =505 nm) and red (peaking at λ =630 nm) light would affect subsequent working memory performance and associated functional brain responses in participants with extreme morning and extreme evening chronotypes. We expected to observe a facilitating effect of blue light in working memory performance with a corresponding pattern of brain responses (Alkozei et al., 2016). Direct comparisons between light exposure at different wavelengths were used to test the specificity of the effect of blue light on brain responses to cognitive tasks (Vandewalle et al., 2007b). To the best of our knowledge this is the first neuroimaging study using within-subject design with various light exposures and visual N-back working memory tasks.

METHODS

Participant selection

During the first stage of the study, a web-based platform on a local server at the Nencki Institute was created in order to select participants with extreme morning (MT) and extreme evening (ET) chronotypes. The selection procedure was based on the Polish version of the Composite Scale of Morningness (CSM -Smith et al., 1989; Jankowski, 2015). The 13-item CSM ranges from 13 (extreme eveningness) to 55 (extreme morningness) points. It provides information on the preferred hours of waking up and retiring to sleep, times of the day subjectively considered by the respondent as optimal for physical and intellectual performance, as well as the levels of arousal and well-being of the subject at different times throughout the day. Scores of 33 points or less for determining ET and 43 points or more for the MT were based on the distribution of scores in a large Polish sample (Jankowski, 2015). Individuals reporting major medical, psychiatric, or neurological conditions, sleep disorders, those who were left-handed, and those who could not take part in MRI studies, were excluded at the first stage of the selection procedure. Furthermore, only males were recruited to the study to avoid confounding effects of sex.

From the total sample of 141 qualified participants, 36 male students (mean age=23; SD=3.09) were enrolled in the experiment on the basis of their CSM scores. However, 12 participants did not attend all experimental sessions, had a large number of missing answers and/or had fallen asleep during the fMRI examination. More precisely, in the MT group, 4 participants were excluded (2 participants had missing data in green and dim conditions, 1 participant did not execute 2-back tasks, and 1 participant did not attend all experimental sessions). In the ET group, 8 participants were excluded (2 participants had missing data in all conditions, 1 participant in blue and green, 1 participant in green, 1 participant in green and dim, 1 participant did not execute 2-back tasks, and 2 participants did not attend all experimental sessions).

Ultimately, 24 males took part in all experimental sessions and were included in the analyses: 12 extreme evening (ET) participants (M age=22.92; SD=1.38) who scored between 16-33 on the CSM (M=22.17; SD=5.50) and 12 extreme morning participants (MT) (M=22.25; SD=2.99) who scored between 42-51 on the CSM (M=45.42; SD 2.75). All participants were right-handed, free from psychiatric, neurological, sleep or major medical disorders. The participants were paid the total of 400 PLN (approximately 100 Euro) as compensation for taking part in all experimental sessions. The study was approved by the Research Ethics Committee at SWPS University of Social Sciences and Humanities, Faculty of Social Sciences and Design in Poznan, Department of Psychology, Poznan, Poland. All participants gave written informed consent to participate in the study.

Materials

Light calibration

Photometric parameters were measured and calibrated using a GL Optics handheld spectrophotometer. The GL Spectics 5.0 Touch was placed at assumed head position during both experimental light exposures. Light irradiance at specific distance was adjusted to match illuminance of 40 lux outside and 20 lux inside the scanner room. See Table I for light parameters during the exposures.

Light exposure before fMRI study

The adaptation and exposure periods were led in an experimental room adjusted for the purpose of the current study. The walls of the room (size 1.4 by 2 meters) were covered with black, sound and light absorbing foam (Fig. 1). The adaptation period lasted 30 min, during which participants were only exposed to an ambient, dim light (<5 lux) (lamp placed on the upper part of the wall not visible in the Fig. 1) behind their heads.

Table I. Light parameters during the exposures.

		Initial ex	kposure	Scanner-room exposure		
	Peak wavelength	Irradiance at X cm [W/m²]	Illuminance [lux]	lrradiance at 10 cm [W/m²]	Illuminance [lux]	
Blue	470 nm	0.74	39.9	0.39	20.0	
Green	505 nm	0.12	40.0	0.07	20.0	
Red	630 nm	0.19	40.4	0.09	20.0	
Dim	-	-	<5	-	<5	



Fig. 1. The experimental room used during light adaptation and expositions periods.

Participants were seated at a desk with 2 light devices (300 × 200 mm) placed at a 45-degree angle to the right and left of center at a distance of approximately 80 cm. Light devices were emitting blue (peaking at λ =470 nm), green (peaking at λ =505 nm) and red (peaking at λ =630 nm) light.

Light exposure during fMRI study

Two light diffusers were installed in the 12-channel MR coil and attached to a standard mirror box. Light diodes were placed outside the scanner room and connected with diffusing chambers with plastic fiber guides. The diode power was precalibrated to match the desired illuminance at a distance of 8, 10, and 12 cm from panels to the nasal bridge which was checked at the beginning of each MR session. After initial exposure outside the scanner room, participants were exposed to the same wavelength in the scanner: blue (peaking at λ =470 nm), green (peaking at λ =505 nm) and red (peaking at λ =630 nm) light. All light devices were custom made by GL Optics company (https://gloptic.com/).

N-back task

In line with previous chronobiological studies, the visual version of the N-back task was used (Schmidt et al., 2015; Alkozei et al., 2016). The task is widely applied for assessing working memory. In the current study, 3 conditions were used (0-back, 1-back and 2-back) increasing in cognitive load. In all conditions, participants were asked to observe a series of white letters (one by one) centered on black screen and respond whenever target stimulus (25% of trials) was the same as the one previously presented in the n trial (n is a pre-specified task condition: 1, 2). In the 0-back condition, participants responded to a pre-specified target letter. In the 1-back condition, the target was a letter presented one trial back. In the 2-back condition, the target was a letter presented two trials back. Participants responded to each stimuli using the right hand index finger to target stimuli and middle finger to non-target stimuli. Wireless response pads from Smit Lab (http://smit-lab.eu/#s2) were used. There were 288 trials in each light condition (single letter presentations). Each block lasted 36 seconds with 16 trials in pseudo randomized order. Letters were presented for 500 ms with inter trial intervals of 2250 ms. The procedure was implemented using Presentation (ver. 18.1 build 03.31.15; Neurobehavioral Systems, Inc., Albany, CA, USA). Both accuracy and reaction times were recorded.

Procedure

Each participant came to the laboratory four times on different days and was exposed to four lighting conditions: blue, green, red and control dim light conditions, according to pseudorandom assignment. There were 3 experimental slots: the first from 8:00 to 10:00, the second from 9:00 to 11:00 and the third from 10:00 to 12:00. Extreme morning types came to the laboratory at 8:00 or at 9:00, while extreme evening types came to the laboratory at 9:00 or at 10:00. Participants arrived at the laboratory approximately 15 min before the experimental session. Before each of the experimental sessions, participants received verbal instructions. Participants were also asked to consume regular levels of caffeine prior to experimental sessions.

At the beginning of each experimental session, all participants filled in the MRI consent form and the Karolinska Sleepiness Scale (KSS -Åkerstedt and Gillberg, 1990) with a 9-point Likert scale to assess an individual's subjective level of sleepiness at a given time. The scale ranges from - "extremely alert" to "very sleepy, great effort to keep alert, fighting sleep". Higher scores on the KSS indicate higher levels of sleepiness. Then, participants were invited to the experimental room (Fig. 1) and instructed not to look directly at the light devices, to relax, open their eyes and maintain a forward gaze. They were seated comfortably at a desk with two light devices. After they assumed the right position, they underwent an adaptation period which lasted 30 min and included being exposed to a dim light. At that time, participants listened to a neutral audiobook in order to prevent them from falling asleep. They were asked to respond on alert prompts randomly presented on the screen in periods from 60 to 300 s to help them stay awake. Participants spent the next 30 min in the same room undergoing an exposure period to one of four conditions. During that time, participants performed a short practice session of the N-back task. Immediately after the exposure period, participants filled in the KSS for the second time and were invited to the MRI scanner. The same light condition as during the exposure period was used in the MR scanner. There were two 8-min runs of N-back tasks, each consisting of 9 blocks. Afterwards, participants exited the scanner and completed the KSS for the third time. We also controlled the sleep schedule of participants the night before the experimental session using questionnaires in order to estimate time since awake.

The research protocol was reviewed and approved by the Commission for Ethics in Scientific Study of the SWPS University in Poznan.

MRI data acquisition

Magnetic resonance imaging was carried out using a 3-Tesla Trio MRI scanner (Siemens Medical Solutions) equipped with a 12-channel phased array coil. A high-resolution T1-weighted image (T1w) was acquired using the following acquisition parameters: TR: 2530 ms, TE: 3.32 ms, flip angle: 7°, 176 slices with a 3D resolution of 1 mm³, field of view: 256 mm, slice thickness: 1 mm. Functional images were acquired using an echo planar imaging pulse sequence with a 3 mm isotropic voxel size (field of view: 216 mm, matrix: 72 × 72, slice thickness: 3 mm, TE: 28 ms, TR: 2500 ms, flip angle: 80°). Forty-one contiguous, oblique-axial images oriented parallel to the anterior-posterior commissural plane were acquired with a total of 195 volumes in each session. Bo field homogeneity maps were acquired with the same spatial parameters as functional scans and TE: 4.5/9.96 ms and TR: 800 ms.

MRI data analysis

Data preprocessing

DICOM series were converted to NIfTI with Horos Bids Output Extension (https://github.com/mslw/ horos-bids-output, dcm2niix engine). Spatial preprocessing was performed using Statistical Parametric Mapping (SPM12, http://www.fil.ion.ucl.ac.uk/spm/). Functional images were corrected for geometrical distortions as well as signal variation related to motion in magnetic field (Andersson et al., 2001), normalized to the MNI space and resliced to 2 × 2 × 2 mm, and smoothed with the 6 mm FWHM Gaussian kernel.

Functional anatomical mapping analysis

Subject-level and group-level analyses were performed using the mass-univariate approach, based on the general linear model, as implemented in SPM12. At the subject level, the N-back task was modelled in a block design (0-, 1-, and 2-back blocks) in a general linear model (GLM) approach. A default canonical hemodynamic response function (HRF) with no derivatives was used to approximate the expected BOLD signal. Motion parameters (translation in x, y, z directions; rotation around x, y, z axes) were inserted into each model as covariates, resulting in 6 regressors of no interest per run. A default high-pass filter cutoff of 128 seconds was used to remove low-frequency signal drifts.

Following Alkozei et al. (2016), contrasts between 2-back > 0-back conditions were specified on an individual basis. At the group level, we performed ANOVA in flexible factorial design (fed with the 2-back>0-back individual contrasts) in order to test the main effect of light/group and interactions. For direct comparison between light, simple t-tests were computed.

A voxel-wise height threshold of p<0.05 corrected for multiple comparisons using the family-wise error (FWE) rate was applied in the whole brain analyses.

Behavioral analysis

Behavioral analyses including KSS, reaction times and correct responses (%) in N-back were conducted using IBM SPSS Statistics 24.0 (2016) software. A repeated measures ANOVA with Greenhouse-Geisser correction and Bonferroni correction for multicomparison was used.

RESULTS

Behavioral results - Karolinska Sleepiness Scale (KSS)

A three way repeated-measures ANOVA with chronotype (2 levels, between subjects factor: M-types vs. E-types), light condition (4 levels, within subjects factor: blue, green, red, dim) measurement time (3 levels, within subjects factor: before session, before fMRI, after session) and the KSS scores as dependent variable showed main effect of measurement time point (TP) p<0.001, $F_{(1.93,42.56)}$ =20.57, η^2 =0.48. Pairwise comparisons showed that participants were more alert at first measurement (M=4.2), than second (M=5.47) p<0.001, and third (M=5.87) p<0.001. There was also a significant main effect of light condition $F_{(2.09,42.55)}$ =3.66, p=0.03, η^2 =0.14 - green light was more stimulating than dim light. Between subjects comparisons showed significant main effect of chronotype on KSS scores p=0.002, $F_{(1,22)}$ =13.08, η 2=0.37, MTs were less sleepy than ETs $p=0.002 (M_{MT}=4.32, M_{ET}=6.04).$

Pairwise comparisons of KSS scores between chronotypes in different light conditions at each level of TP variable showed that MT felt less sleepy than ET in blue p=0.02 ($M_{MT}=3.08$, $M_{ET}=4.83$), green p=0.003 ($M_{MT}=2.83$, M_{ET} =5.17), and red p<0.001 (M_{MT} =3.17, M_{ET} =5.67) light conditions in TP 1. In TP 2 and TP 3 there were significant differences between MT and ET in green (TP2: p<0.001, M_{MT} =3.67, M_{ET} =6.58; TP3: p=0.04, M_{MT} =4.83, M_{ET} =6.83) and dim light conditions (TP2: p=0.04, M_{MT} =5.5, M_{ET} =6.75; TP3: p=0.02, M_{MT} =5.33, M_{ET} =7.17). We also observed a difference between TP 2 and MT groups between green and dim conditions p<0.001(M_{Green} =3.67, M_{Dim} =5.5).

Pairwise comparisons of KSS scores between TPs in different chronotypes and light conditions showed differences between TP1 and TP3 (p=0.004, M_{TP1} =3.08, M_{TP3} =5.0) in the MT group blue light condition. In the red condition, the MT group had lower scores in TP1 than TP2 and TP3 (consecutively: p_{TP1vsTP2} =0.002, p_{TP1vsTP3} =0.03, M_{TP1} =3.17, M_{TP2} =5.17, M_{TP3} =5.17). In green light, both chronotype groups were more alerted in TP1 than TP3 (MT: p=0.01, M_{TP1} =2.83, M_{TP3} =4.83, ET: p=0.04, M_{TP1} =5.17, M_{TP3} =6.83,). Similarly, in the dim light condition, both groups were more alerted in TP1 than TP3 (MT: p=0.02, M_{TP1} =3.92, M_{TP3} =5.33, ET: p=0.001, M_{TP1} =5.0 M_{TP3} =7.17), or TP2 (MT: p=0.002, M_{TP1} =3.92, M_{TP2} =5.5, ET: p=0.001, M_{TP1} =5.0 M_{TP2} =6.75). Fig. 2 presents a summary of the results from KKS.

In addition, we calculated the time since awake based on questionnaires and we found no significant differences between groups. On average, the MT group woke up at 6:28 (SD=28 min) and started experimental sessions at 8:12 (SD=24 min) while the ET group woke at 7:46 (SD=43) and started experimental sessions at 9:40 (SD=31).

Behavioral results - N-back task

In the N-back task, we found differences only in reaction times (RT). We also analysed accuracy using percentage of correct responses (%) but, because of the ceiling effect, there were no significant findings (mean accuracy 0-b=87.3%; 1-b=86.2%; 2-b=86.7%).

There was only one significant main effect for RTs: effect of difficulty, p<0.001, $F_{(1.13,24.81)}$ =16.17, η^2 =0.42. As the difficulty of the task increased, so did reaction times. In the 0-back condition, participants were faster than in the 1-back p<0.001 (M_{0-b} =520.26 ms, M_{1-b} =551.51 ms) and 2-back p<0.001 (M_{2-b} =600.28 ms). RTs in the 1-back were also different from the 2-back p<0.007. Results from RT in N-back task are presented in Fig. 3 and Table II.

fMRI results

Main effect of light was computed using ANOVA in flexible factorial design (with 4 types of light and 2 groups) and revealed no significant results surviving correction for multiple comparisons. However, taking into consideration the previous work of Schmidt and colleagues (2015) we expected to find differences between the MT and ET groups and we computed additional T-tests. We found higher brain activity for the MT in comparison to ET chronotype when pooling data from all light conditions in several brain regions

(Table III and Fig. 4). There were no significant differences for the opposite contrast (ET > MT).

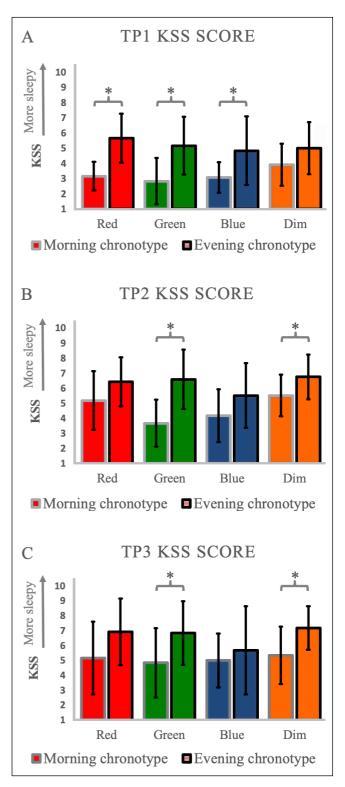


Fig. 2. Summary of results for Karolinska Sleepiness Scale. Panel A, Panel B, Panel C – represents each time point (TP) of the study. Error bars represent standard deviations.

Table II. Summary of behavioural results from all participants in the N-back task. RT – reaction time; ns – non significant.

Light colour		Blue			Green	
Difficulty	0-back	1-back	2-back	0-back	1-back	2-back
Mean RT	516.12	551.85	595.19	512.85	549.09	599.02
Comparison	0-b <i>vs.</i> 1-b	0-b <i>vs.</i> 2-b	1-b <i>vs.</i> 2-b	0-b <i>vs.</i> 1-b	0-b <i>vs.</i> 2-b	1-b vs. 2-b
p-value	p=0.003	p<0.001	p=0.01	p=0.007	p=0.003	p=0.006
Light colour		Red			Dim	
Difficulty	0-back	1-back	2-back	0-back	1-back	2-back
Mean RT	526.01	555.86	602.77	520.58	549.23	604.14
Comparison	0-b <i>vs.</i> 1-b	0-b <i>vs.</i> 2-b	1-b <i>vs.</i> 2-b	0-b <i>vs.</i> 1-b	0-b <i>vs.</i> 2-b	1-b <i>vs.</i> 2-b
p-value	p=0.003	p=0.01	ns.	p=0.003	p=0.002	p=0.007

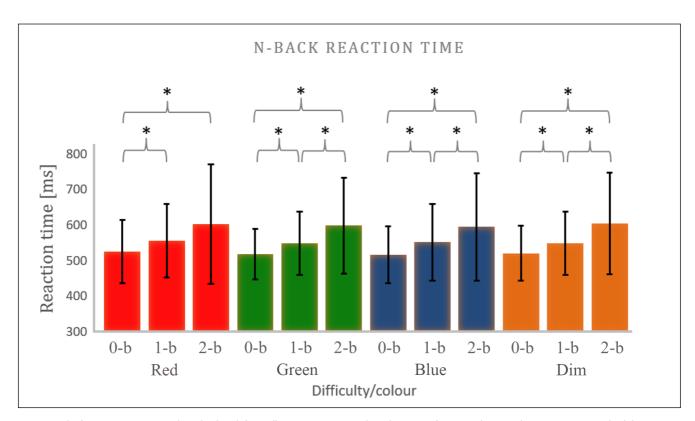


Fig. 3. Results from reaction time in the N-back task from all participants. Asterisks indicate significant results. Error bars represent standard deviations.

DISCUSSION

The aim of the current study was to examine the influence of light exposure at different wavelengths on behaviour and brain response in selected participants with extreme morning and extreme evening chronotypes. Here we employed blue (peaking at λ =470 nm), green (peaking at λ =505 nm) and red (peaking at λ =630 nm) lights and the well-established N-back test, allowing assessment of working memory. We anticipated that we would be able to replicate results suggesting the facilitating effect of blue light on working memory performance with a corresponding pattern of brain responses - increased prefrontal activation (Alkozei et al., 2016). We employed an experiment varying light exposure in a within-subjects design. In addition, we used the Karolinska Sleepiness Scale (KSS) which assesses a subjective level of sleepiness at a given time (Åkerstedt and Gillberg, 1990). Overall, in the morning sessions, the level of alertness

Table III. Peak level activations for extreme morning (MT) in comparison to extreme evening (ET) chronotype for data pooled from all light conditions.
Statistical threshold at p<0.05 corrected for multiple comparisons using the family-wise error (FWE).

			MNI Coordinates		
Region Label	Extent	t-value	x	у	Z
R Precentral Gyrus	176	6.372	58	-2	42
L Superior Medial Gyrus	46	5.825	-6	14	46
L Middle Occipital Gyrus	102	5.658	-40	-82	18
L Middle Frontal Gyrus	111	5.603	-26	14	48
R Superior Occipital Gyrus	44	5.495	28	-76	48
L Superior Frontal Gyrus	34	5.467	-26	52	8

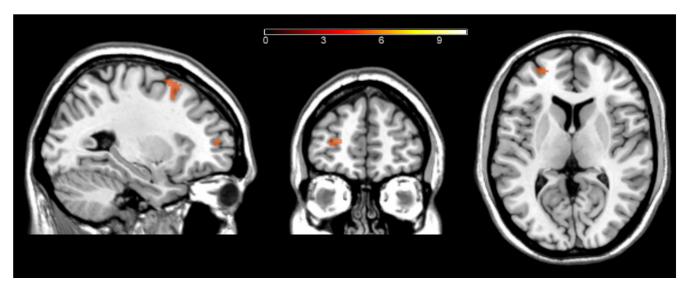


Fig. 4. Results for data pooled from all light conditions representing higher brain activity for extreme morning (MT) in comparison to extreme evening (ET) chronotype. Statistical threshold at p<0.05 corrected for multiple comparisons using the family-wise error (FWE). Finally, we computed analyses using the region of interest (ROI) approach including brain structures reported in previous studies (Schmidt et al., 2015; Alkozei et al., 2016). We also did not find any significant result corrected for multiple comparisons.

measured with the self-assessment KSS scale was significantly higher in extremely morning type in comparison to extremely evening type which is consistent with previous findings (Kaida et al., 2006). Since we did not find significant differences in time since awake, we believe the KSS score showed expected differences in alertness levels between the chronotypes. Namely, previous research showed that evening-types exhibit lower levels of energetic arousal/alertness as compared to morning-types in the morning and afternoon (Jankowski and Ciarkowska, 2008), so the difference in KSS scores during morning hours is in line with this finding.

In the N-back task we did not find significant differences in performance between the groups or types of light exposure, nor an interaction between these two factors. We were only able to observe a significant ef-

fect of N-back task difficulty on reaction times which is in line with the majority of studies using this working memory paradigm (Yaple et al., 2019). This result also confirms the validity of the experimental paradigm used in current study. The absence of a significant effect of light exposure is contradictory to the previous findings of Alkozei and colleagues (2016). They showed, using a similar visual N-back paradigm, that blue light in comparison to amber light has a subsequent beneficial effect on working memory performance.

At the neuronal level, we did not replicate findings showing increased activation within prefrontal regions (Alkozei et al., 2016) in the case of blue light exposure which was expected to have an enhancing effect on accelerated cognition and brain function. In this study, however, a between group design was employed, which might have revealed already exist-

ing group differences independent of light exposure. The effect of blue light has also been reported in other studies. However, most of them included only one control condition of different wavelength (Prayag et al., 2019), in contrast to the spectrum of lights employed in the current study. One exception is the study of Vandewalle and colleagues (2007a), who used alternating violet (430 nm), blue (473 nm), or green (527 nm) mono-chromatic, 50 s light exposures and an auditory working memory N-back task. They found, at the behavioural level, that performance (reaction times and accuracy) was not affected by the light exposure condition. At the neuronal level it was only observed that during the task with blue light, as compared to violet light, increased activity was observed in the left middle frontal gyrus, left thalamus and bilaterally in the brainstem area, consistent with activation of the locus coeruleus (Vandewalle et al., 2007b).

Additional analyses, with a direct comparison between chronotypes for data from each colour, were pooled together to reveal higher brain activity for extreme morning as compared to extreme evening chronotype in several prefrontal and occipital brain areas. These results are in line with the study of Schmidt and colleagues (2015) indicating increased strategic or attentional recruitment of prefrontal areas, implicated in compensating working memory load in the morning chronotype.

Limitation and future directions

There are several limitations of the current study. Firstly, only a visual N-back was used to assess the influence of different lights on working memory performance. We did not use exactly the same wavelengths of lights as the work of Alkozei and colleagues (2016) and the number of subjects in each group was relatively small. Therefore, further studies are needed to confirm our results. We also postulate that subsequent studies should extend experimental paradigms by employing working memory tests in different modalities. We also think that both EEG and fMRI methodology should be engaged in order to link spatial and time resolution of both methods.

CONTRIBUTION

Experiment conception and design: BK, DD, KR, JM, KSJ, MW AM, AW; experiment execution: BK, DD, KR; data analysis: BK, DD, KR, MW, AM; manuscript draft: BK, DD, KR, KSJ, AW, AM; revision and proofreading: BK, DD, KR, JM, KSJ, MW AM, AW.

ACKNOWLEDGEMENTS

This paper is based on the results of a research task carried out within the scope of the fourth stage of the National Programme "Improvement of safety and working conditions" partly supported in 2017-2019 - within the scope of research and development - by the Ministry of Science and Higher Education / National Centre for Research and Development. The Central Institute for Labour Protection - National Research Institute (CIOP-PIB), is the Programme's main co-ordinator. The study was conducted with the aid of CePT research infrastructure purchased with funds from the European Regional Development Fund as part of the Innovative Economy Operational Programme, 2007-2013.

REFERENCES

Åkerstedt T, Gillberg M (1990) Subjective and objective sleepiness in the active individual. Int J Neurosci 52: 29-37.

Alkozei A, Smith R, Pisner DA, Vanuk JR, Berryhill SM, Fridman A, Shane BR, Knight SA, Killgore WDS (2016) Exposure to blue light increases subsequent functional activation of the prefrontal cortex during performance of a working memory task. Sleep 39: 1671-1680.

Andersson JLR, Hutton C, Ashburner J, Turner R, Friston K (2001) Modeling geometric deformations in EPI time series. Neuroimage 13: 903-919.

Berson D, Dunn F, Takao M (2002) Phototransduction by retinal ganglion cells that set the circadian clock. Science 295: 1070-1073.

Borbély AA, Daan S, Wirz-Justice A, Deboer T (2016) The two-process model of sleep regulation: a reappraisal. J Sleep Res 25: 131–143.

Cajochen C (2007) Alerting effects of light. Sleep Med Rev 11: 453-464.

Dijk DJ, Archer SN (2009) Light, sleep, and circadian rhythms: together again. PLoS Biol 7: e1000145.

Facer-Childs ER, Boiling S, Balanos GM (2018) The effects of time of day and chronotype on cognitive and physical performance in healthy volunteers. Sports Med Open 4: 47.

Fafrowicz M, Golonka K, Marek T, Mojsa-Kaja J, Tucholska K, Oginska H, Urbanik A, Orzechowski T (2009) Diurnal variability of human operator attention disengagement and chronotype: an fMRI-based case study. Theor Issues Ergon Sci 10: 545-557.

Gorfine T, Yeshurun Y, Zisapel N (2007) Nap and melatonin-induced changes in hippocampal activation and their role in verbal memory consolidation. J Pineal Res 43: 336-342.

Gorfine T, Zisapel N (2009) Late evening brain activation patterns and their relation to the internal biological time, melatonin, and homeostatic sleep debt. Hum Brain Mapp 30: 541-552.

Holzman DC (2010) What's in a color? The unique human health effect of blue light. Environ Health Perspect 118: A22-A27.

Jankowski KS, Ciarkowska W (2008) Diurnal variation in energetic arousal, tense arousal and hedonic tone in extreme morning and evening types. Chronobiol Int 25: 577-595.

Jankowski KS, Zajenkowski M (2016) The role of morningness and endurance in mood and attention during morning and evening hours. J Individual Differ 37: 73-80.

Jankowski KS (2015) Composite Scale of Morningness: Psychometric properties, validity with Munich ChronoType Questionnaire and age/sex differences in Poland. Eur Psychiatry 30: 166-171.

Kaida K, Takahashi M, Åkerstedt T, Nakata A, Otsuka Y, Haratani T, Fukasawa K (2006) Validation of the Karolinska sleepiness scale against performance and EEG variables. Clin Neurophysiol 117: 1574-1581.

- Peres I, Vetter C, Blautzik J, Reiser M, Pöppel E, Meindl T, Roenneberg, T, Gutyrchik E (2011) Chronotype predicts activity patterns in the neural underpinnings of the motor system during the day. Chronobiol Int 28: 883–889.
- Prayag AS, Münch MY, Aeschbach D, Chellappa SL, Gronfier C (2019) Light modulation of human clocks, wake, and sleep. Clocks Sleep 1: 193–208.
- Ramírez C, Talamantes J, García A, Morales M, Valdez P, Menna-Barreto L (2006) Circadian rhythms in phonological and visuospatial storage components of working memory. Biol Rhythm Res 37: 433–441.
- Schmidt C, Collette F, Cajochen C, Peigneux P (2007) A time to think: Circadian rhythms in human cognition. Cogn Neuropsychol 24: 755–789.
- Schmidt C, Collette F, Leclercq Y, Sterpenich V, Vandewalle G, Berthomier P, Berthomier C, Phillips C, Tinguely G, Darsaud A, Gais S, Schabus M, et al. (2009) Homeostatic sleep pressure and responses to sustained attention in the suprachiasmatic area. Science 324: 516–519.
- Schmidt C, Collette F, Reichert CF, Maire M, Vandewalle G, Peigneux P, Cajochen C (2015) Pushing the limits: chronotype and time of day modulate working memory-dependent cerebral activity. Front Neurol 6: 199.
- Schmidt C, Peigneux P, Leclercq Y, Sterpenich V, Vandewalle G, Phillips C, Berthomier P, Berthomier C, Tinguely G, Gais S, Schabus M, Desseilles M,

- et al. (2012) Circadian preference modulates the neural substrate of conflict processing across the day. PLoS One 7: e29658.
- Smith CS, Reilly C, Midkiff K (1989) Evaluation of three circadian rhythm questionnaires with suggestions for an improved measure of morningness. J Appl Psychol 74: 728–738.
- Tassi P, Pellerin N, Moessinger M, Eschenlauer R, Muzet A (2000) Variation of visual detection over the 24-hour period in humans. Chronobiol Int 17: 795–805.
- Vandewalle G, Gais S, Schabus M, Balteau E, Carrier J, Darsaud A, Sterpenich V, Albouy G, Dijk DJ, Maquet P (2007a) Wavelength-dependent modulation of brain responses to a working memory task by daytime light exposure. Cereb Cortex 17: 2788–2795.
- Vandewalle G, Schmidt C, Albouy G, Sterpenich V, Darsaud A, Rauchs G, Berken P-Y, Balteau E, Degueldre C, Luxen A, Maquet P, Dijk D-J (2007b) Brain responses to violet, blue, and green monochromatic light exposures in humans: prominent role of blue light and the brainstem. PLoS One 2: e1247.
- Yaple ZA, Stevens WD, Arsalidou M (2019) Meta-analyses of the n-back working memory task: fMRI evidence of age-related changes in prefrontal cortex involvement across the adult lifespan. Neuroimage 196: 16–31.