Different colors of light lead to different adaptation and activation as determined by high-density EEG

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A B S T R A C T
Light adaptation is crucial for coping with the varying levels of ambient light. Using high-density electroencephalography (EEG), we investigated how adaptation to light of different colors affects brain responsiveness. In a within-subject design, sixteen young participants were adapted first to dim white light and then to blue, green, red, or white bright light (one color per session in a randomized order). Immediately after both dim and bright light adaptation, we presented brief light pulses and recorded event-related potentials (ERPs). We analyzed ERP response strengths and brain topographies and determined the underlying sources using electrical source imaging. Between 150 and 261 ms after stimulus onset, the global field power (GFP) was higher after dim than bright light adaptation. This effect was most pronounced with red light and localized in the frontal lobe, the fusiform gyrus, the occipital lobe and the cerebellum. After bright light adaptation, within the first 100 ms after light onset, stronger responses were found than after dim light adaptation for all colors except for red light. Differences between conditions were localized in the frontal lobe, the cingulate gyrus, and the cerebellum. These results indicate that very short-term EEG brain responses are influenced by prior light adaptation and the spectral quality of the light stimulus. We show that the early EEG responses are differently affected by adaptation to different colors of light which may contribute to known differences in performance and reaction times in cognitive tests.

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Introduction

Light has direct effects on many non-visual functions including hormonal secretion, alertness, and heart rate (Cajochen, 2007). The recently discovered class of intrinsically photosensitive retinal ganglion cells (ipRGCs), having maximal sensitivity to blue light in the range of 480 nm, is likely the principal mediator of these effects in humans (Berson et al., 2002; Hattar et al., 2002). The most compelling evidence comes from studies which have shown that, indeed, blue, compared to green and red light has a greater influence on circadian rhythms, pupil light reflexes, heart rate, and hormonal secretion (Cajochen, 2007; Lockley, 2008; Münch and Kawasaki, 2013). Effects of blue light are also evident in neural responses. For example, within one minute after light onset, monochromatic blue light elicits stronger brain activation than green or red light in the brainstem and thalamus (Vandewalle et al., 2009). Interestingly, even in blind persons with no functional rod or cone photoreceptors (but intact light perception via ipRGCs), EEG brain activation is higher for blue than green light exposure when performing an auditory task (Vandewalle et al., 2013).

Environmental light changes dynamically, varying between 4 lx illuminance (moon light) and 100,000 lx (clear sunny sky). Adaptation is crucial to allow the visual system to operate efficiently throughout this range of illuminance levels. Light adaptation occurs at many levels, including up- and down-regulation of rod and cone photoreceptor and retinal ganglion cell sensitivity (Shapley and Enroth-Cugel, 1984). This adaptation is evident in event-related potentials (ERPs) to stimuli presented after adaptation. Bright light exposure after dark adaptation leads to fast non-linear photoreceptor saturation (Hecht et al., 1937) and attenuates ERPs in the primary visual cortex (Spafford and Lu, 1989). There is evidence that ipRGCs modulate both rod and cone sensitivity via dopaminergic amacrine cells (Zhang et al., 2008). However, the exact characteristics are largely unknown. For example, it remains unclear whether blue light leads to an increase or decrease in ipRGC cell sensitivity.

Given these complex neural characteristics, we asked the question whether adaptation to different wavelengths of light leads to different evoked brain responses. Our first question was how adaptation to dim and bright light influences the response strength to subsequent light. Only a few EEG studies have addressed this question [e.g., (Monnier et
al. 1964)]. Our second question was whether blue light leads to less adaptation than red, white, and green light because of its greater alerting and activating nature mediated by the ipRGC system. Reaction times in sustained vigilance tests are faster under constant monochromatic blue light conditions, suggesting that cognitive processing occurs more rapidly (Lockley et al., 2006).

Material and methods

Participants

Sixteen healthy volunteers participated [3 female; age range: 19–27 y; 22.5 ± 2.5 y (mean ± SD)]. All participants were non-smokers and free from medical, psychiatric and sleep disorders, as assessed by an interview and three different screening questionnaires [entrance questionnaire, Pittsburgh Sleep Quality Index (Buysse et al., 1989) and Horne–Ostberg Morning–Eveningness Questionnaire (Horne and Ostberg, 1976)]. None of the volunteers was an extreme chronotype, worked night shifts or had crossed more than one time zone during the last two months before the study began. A thorough ophthalmological examination was carried out (Hôpital Ophtalmoïque Jules-Gonin, Lausanne, Switzerland) before and after the study. None of the participants had any ocular pathology; they all had normal fundoscopy, visual acuity, and color vision. For one week prior to the study, volunteers abstained from excessive alcohol and caffeine consumption and kept a regular sleep–wake schedule (with bed- and wake times within ±30 min of self-selected target times), verified by a wrist monitor (Daqtix®, Oetzen-Süttorf, Germany) and a sleep diary. Between subjects, bed times ranged from 22:49 to 00:59 (hours:minutes; 23:51 ± 37 min) and the wake time ranged from 6:58 to 8:36 (7:45 ± 31). For each subject, habitual bed and wake times remained within a narrow time range; they varied on average ±17 min (bed time) and ±18 min (wake time) between sessions. Time in bed was on average 7:54 ± 9 min (n = 16). All volunteers gave written informed consent. The procedures were approved by the local Ethical Review Board and in agreement with the Declaration of Helsinki.

Study design

We used a randomized within-subject study design where participants adapted first to dim white light and then to either blue, green, red, or white bright light (one color per session). The study consisted of four sessions, separated by at least one day. Participants were admitted to the laboratory at noon (approximately 3.5–5 h after wake time). After mounting of the electrode cap, participants were exposed to dim (<6 lx) polychromatic white light for 25 min. After the adaptation period, we presented short light pulses of one out of four different colors to both eyes and recorded event-related potentials (ERPs). This recording is referred to as dim light adapted ERP (ERP-DA). We used monochromatic blue (480 nm), green (555 nm), red (620 nm), or polychromatic white light (Fig. 1). Per session, only one color was presented. For each participant, the order of colors was randomized. Next, the participants were exposed to constant monochromatic or white bright light for 60 min. The same color was used as for the ERP recordings. After this, participants underwent a second ERP recording identical to the first one, referred to as bright light adapted ERP (ERP-LA).

Lighting conditions

The participants were seated in front of an Ulbricht Sphere which provided a homogenous luminous distribution. A polychromatic white light flux was generated by an arc-ozone-free Xenon lamp (1200 W), and the monochromatic lights with a grating monochromator (L.O.T. Oriel-Suisse, Romanel-sur-Morges, Switzerland), at equal photon densities (2.8 × 10¹⁳ photons/cm²/s; ±15 nm half-peak bandwidth). Participants were asked to position their chin on a chinrest and to look straight in the sphere without moving their head. During the ERP recordings, brief exposures to light were produced by opening and closing a mechanical shutter, operated by customized scripts via a PC. Per color condition, 160 light flashes lasting 150 ms were presented, with randomly chosen inter-stimulus intervals of 1500–2500 ms, leading to ERP recordings lasting between 5 and 7 min. Participants were asked to keep their eyes open during the ERP recordings and to blink only during the (dark) inter-stimulus intervals.

High-density EEG recording

Continuous EEG was recorded with a BioSemi Active2 system (http://www.biosemi.com) with 128 Ag-AgCl sintered active electrodes (located in a cap according to the 10–20 system) and four additional electrodes to register the electrooculogram (EOG). All electrodes were referenced to a common mode sense (CMS) electrode and grounded to a passive electrode. The EEG was recorded with a sampling rate of 2048 Hz and later offline down-sampled to 512 Hz. All EEG recordings were DC corrected and band-pass filtered between 1 and 40 Hz by using a 2nd order Butterworth filter (−12 dB/octave roll-off). A notch filter removed the 50 Hz noise from electrical power supplies. Artifacts were removed by applying semi-automatic artifact rejection with a ±75 μV amplitude threshold. On average, 25.6% of the trials were excluded from further analysis (41 out of 160 trials). The exclusions were mostly due to blink artifacts and occurred similarly between colors (Kruskal–Wallis test, p = 0.3) and between ERP-DA and ERP-LA (p = 0.08). Noisy electrodes were excluded from artifact detection and later interpolated using 3D splines.

Global field power analysis

Global field power (GFP) is defined as the standard deviation of electrical potentials across all EEG scalp electrodes at a given time, and reflects the neuronal response strength throughout the brain (Lehmann and Skrandies, 1980). We computed GFP in the interval

![Fig. 1. Overview of the study protocol. During the first hour of the study session, participants were exposed to “normal” room light (≈90 lx at the eye level in a vertical direction; white areas). Next, dim light was presented for 25 min (polychromatic white light; <6 lx; light gray area). The first ERP recording was performed (ERP dim light adapted = ERP-DA), followed by one hour of constant bright light exposure (darker gray area). Then, a second ERP recording after light adaptation (= ERP-LA) took place. Note that the two ERP recordings and the constant bright light exposures were done with monochromatic green, blue, red and polychromatic white light at the same photon densities. Participants were exposed to one color in each of the four study sessions.](image-url)
from 100 ms pre-stimulus to 400 ms post-stimulus onset after dim light adaptation (ERP-DA) as well as after bright light adaptation (ERP-LA) for all colors (blue, green, red and white). We applied mixed linear regression models to the data with the factors ‘color’ and ‘adaptation’, and adjusted \( p \)-values for multiple comparisons between conditions per time episode (Tukey–Kramer Test).

Topographic analysis of event-related potentials
We examined spatial variations of the electrical field potentials in the EEG scalp topography over time. In humans and non-human primates, electrical scalp potentials do not randomly vary over time, but tend to be stable during short times (\(< 1 \) s), and change by brief intrusions of instability (Michel et al., 2001, 2004; Murray et al., 2008). These variations of stable spatial configurations in electrical scalp potentials are assumed to indicate changes in underlying neuronal activation (Michel et al., 2004).

In order to determine the sequence of discrete spatial configurations across study participants and conditions, we segmented the grand averages per condition into a limited number of template maps. We applied the Atomize and Agglomerate Hierarchical Clustering (AAHC) algorithm (Murray et al., 2008) to obtain a limited number of different template maps. To identify the set of template maps which best represented our data across all conditions, we determined the absolute minimum of the Cross Validation (CV) value (Pascual-Marqui et al., 1995). The CV value is the ratio between the global explained variance and the degrees of freedom in the model (Murray et al., 2008). Template maps with a correlation larger than 80% were merged together, while maps shorter than 20 ms were merged into the most similar neighboring maps. The minimum CV value provides a data-driven way to choose a set of template maps, resulting in a low number of maximally distinct template maps.

To determine contributions of individual scalp topographies to each of the template maps, we compared the single-subject averages with the template maps. Each time point was labeled by the map with the highest spatial correlation (‘backfitting’). The individual durations of the template maps were compared between lighting and adaptation conditions by applying mixed regression analyses and adjusted \( p \)-values for multiple comparisons between conditions per time episode (Tukey–Kramer Test).

Source analyses
We used a Local Autoregressive Average algorithm (LAURA; Grave de Peralta et al., 2001; Michel and Murray, 2012), embedded in the software Cartool (v. 3.52; by Denis Brunet; brainmapping.unige.ch/cartool), to create the inverse solutions. In order to do so, we defined a solution space of 4995 evenly spread source points within the gray matter of the Montreal Neurological Institute’s (MNI) 152 template brain. We created an analytical head model using a manifold of locally adapted spheres (Brunet et al., 2011) to calculate the lead field for each of the 128 electrodes. To co-register the 128 electrode locations with the template brain, we determined 3D landmarks for the 128 scalp electrode positions by applying in-house software and a complementary infrared- and video-based motion tracker system (EEG-Navi, M. Repnow, LPSY, EPFL, Lausanne v.1; 2012 and Polaris; Northern Digital Inc.). We used time intervals with significant GFP differences as periods of interest for the source analysis. In those time intervals, all source points were compared using paired \( t \)-tests and Bonferroni corrected \( p \)-values with a family-wise error rate of 10% (see also below for further explanation). For light adaptation effects between ERP-DA and ERP-LA, normalized GFP values per time frame were applied for comparisons between two conditions. To assign the Talairach brain atlas coordinates (\( xyz \)) we used the software Talairach Client (Lancaster et al., 2000).

Statistics
EEG data processing and analyses were performed with the software Cartool. Statistical analyses for GFP comparisons were performed by using the software package SAS (SAS Institute Inc., Cary, NC, USA; version 9.3). Data from GFP comparisons were log-transformed prior to mixed linear regression analysis (PROC MIXED) with the two repeated factors ‘color’ (blue, green, red and white light stimuli) and ‘adaptation’ (ERP-DA vs. ERP-LA). For post-hoc tests, we applied the Tukey–Kramer for significant GFP comparisons and topographic analysis (\( p \)-values were adjusted for multiple comparisons). Based on these post-hoc tests (from GFP comparisons) we identified whether GFP was significantly higher or lower between conditions. In order to determine the source points of these GFP differences by inverse solutions, we applied one-tailed paired \( t \)-tests between ERP-DA and ERP-LA, and between colors. Justification for using the one-tailed \( t \)-test was given by the fact that we already identified the direction of the GFP effects and the IS should go in the same direction. We used Bonferroni correction for multiple comparisons across all source points.

Results
Global field power (GFP) in the range from 150 to 261 ms was lower after bright than dim light adaptation (Fig. 2). This effect was largest with monochromatic red light and smallest with monochromatic blue light.

![Fig. 2. Global field power (GFP), averaged across participants for each of the four light conditions and two adaptation conditions. Upper part, ERPs after dim light adaptation (ERP-DA); lower part, ERPs after bright light adaptation (ERP-LA; \( n=16; \; +\text{SEM})

Black squares at the bottom indicate significant differences between ERP-DA and ERP-LA (main effect of adaptation). Dark squares show main effects of ‘color’ and light gray squares show significant interactions between the factors ‘color’ and ‘adaptation’. Vertical dashed lines show the stimulus onset (\( =0 \text{ ms} \)).]
Fig. 3. A–D: Global field power responses to different light conditions after dim and after bright light adaptation. Global field power (GFP) for monochromatic red (A), green (B) and blue (C), and for polychromatic white light (D). For each color, ERPs after dim light adaptation (ERP-DA) and after bright light adaptation (ERP-LA) are presented with the respective lighter and darker colors. Light gray squares at the bottom of each graph indicate significant differences, separately for each color (n = 16; mean ± or − SEM). Vertical dashed black lines indicate light stimulus onset (=0 ms).

Fig. 4. A–B: Microstate analysis and temporal distribution across lighting conditions. A: The eight distinct template maps (maps 1–8) which best explained changes in EEG potential topographies across light conditions, as determined by segmentation analysis in the time interval from −100 ms to 400 ms after stimulus onset. The template map numbers (and their background colors at the top) correspond to the temporal distribution (see 4B). The red color in the template maps indicates positive EEG scalp potentials, and the blue color indicates negative EEG scalp potentials. B: The temporal distribution of template maps 1–8 is shown for global field power (GFP). Results from blue, green, red and white light stimuli are illustrated in rows 1–4. The left column shows ERPs after dim light adaptation (ERP-DA) and the second column those after the bright light adaptation (ERP-LA; N = 16). The numbers and colors in the area under the GFP correspond to the respective template maps (see 4A).
light (main effect of ‘adaptation’; p < 0.05, Fig. 3, Supplemental Table 1). Within the first 100 ms, GFP was higher for blue, green, and white light than for red light, indicating increased neuronal responses after bright light adaptation (Figs. 2 and 3). Specifically, we found that the GFP was higher with green (39–78 ms), blue (46–62 ms), and white light (52–76 ms), than with red light (post-hoc analysis with Tukey–Kramer

<table>
<thead>
<tr>
<th>X</th>
<th>Y</th>
<th>Z</th>
<th>Brain source</th>
<th>Time interval condition</th>
</tr>
</thead>
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<tr>
<td>−48</td>
<td>−35</td>
<td>−22</td>
<td>Left cerebrum, temporal lobe, fusiform gyrus</td>
<td>150–261 ms: ERP-DA &gt; ERP-LA</td>
</tr>
<tr>
<td>−48</td>
<td>28</td>
<td>13</td>
<td>Left cerebrum, frontal lobe, inferior frontal gyrus/orbital gyrus</td>
<td></td>
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<tr>
<td>−54</td>
<td>22</td>
<td>19</td>
<td>Left cerebrum, frontal lobe inferior gyrus</td>
<td></td>
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<td>−28</td>
<td>60</td>
<td>11</td>
<td>Left cerebrum, middle frontal gyrus</td>
<td></td>
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<tr>
<td>9</td>
<td>−31</td>
<td>70</td>
<td>Right cerebrum, frontal lobe, paracentral lobulus</td>
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<td>9</td>
<td>34</td>
<td>−4</td>
<td>Right cerebrum, anterior cingulate gyrus</td>
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<td>−28</td>
<td>−71</td>
<td>18</td>
<td>Left cerebrum, occipital lobe, precuneus</td>
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<tr>
<td>−41</td>
<td>−71</td>
<td>6</td>
<td>Left cerebrum, occipital lobe, middle occipital gyrus</td>
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<tr>
<td>48</td>
<td>−35</td>
<td>−28</td>
<td>Right cerebellum, anterior lobe, culmen</td>
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<tr>
<td>−35</td>
<td>18</td>
<td>55</td>
<td>Left cerebrum, frontal lobe, middle frontal gyrus</td>
<td>39–78 ms ERP-LA: Green &gt; Red</td>
</tr>
<tr>
<td>3</td>
<td>−20</td>
<td>27</td>
<td>Right cingulate gyrus</td>
<td></td>
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<td>−3</td>
<td>−26</td>
<td>28</td>
<td>Left cingulate gyrus</td>
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<td>−35</td>
<td>−8</td>
<td>15</td>
<td>Left insula</td>
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<td>−9</td>
<td>−34</td>
<td>−6</td>
<td>Left cerebellum, anterior lobe, culmen</td>
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<tr>
<td>−41</td>
<td>11</td>
<td>50</td>
<td>Left cerebrum, frontal lobe, middle frontal gyrus</td>
<td>46–62 ms ERP-LA: Blue &gt; Red</td>
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<tr>
<td>−41</td>
<td>18</td>
<td>49</td>
<td>Left cerebrum, frontal lobe, superior gyrus</td>
<td></td>
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<tr>
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<td>34</td>
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<td>Left cerebrum, frontal lobe, Inferior frontal gyrus</td>
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<tr>
<td>−48</td>
<td>53</td>
<td>6</td>
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<td>22</td>
<td>64</td>
<td>−22</td>
<td>Right cerebrum, frontal lobe, superior gyrus</td>
<td>52–76 ms ERP-LA: White &gt; Red</td>
</tr>
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Table 1
Summary from inverse solutions (LAURA).
Results from inverse solution analysis (LAURA) are shown with the X, Y, Z (Talairach-) coordinates (first three columns), indicated with the corresponding brain regions (fourth column) and the respective time interval and light conditions (fifth column). Time intervals are based on significant differences in global field power (see supplemental Table 1).
In order to differentiate topographic changes between the red color and the other light conditions where we found lower GFP with red light, we compared the duration of the three template maps (maps 1–3) present in the interval from 39 to 78 ms after light onset (Fig. 6). We found that template map 1 lasted longer in the green than in the red color conditions (Fig. 6; middle). Template map 3 lasted longer in the blue than the red light condition (Fig. 6; top). For red light, template map 2 lasted longer than for blue, green and white light responses ($p < 0.05$; Fig. 6; top, middle and bottom).

To determine the brain sources underlying the ERPs, we focused on the time intervals where the most prominent topographic changes occurred after bright light adaptation (Figs. 7A, B). We found significantly greater current densities for green light than for red light in the left middle frontal gyrus of the frontal lobe, the left and right cingular gyrus, the left insula and in the left anterior lobe of the cerebellum (from 39 ms to 78 ms; top). For blue light, there were higher current densities in the left middle, superior and inferior gyrus of the frontal lobe than for red light (from 46 ms to 62 ms after stimulus onset). When comparing white with red light stimuli (from 52 ms to 76 ms after stimulus onset; bottom), we found greater neuronal activation in the inferior part of the right frontal lobe for white light (Fig. 7C).

**Discussion**

We conducted a high-density EEG study where participants were first adapted to dim white light and then were probed with flashes of one color of light (blue, green, red, and white light). Next, participants were adapted to the same color with bright light and again probed with flashes of this color and the EEG was recorded for both ERPs. In the range from 150 to 261 ms, global field power (GFP) was lower after bright light adaptation than after dim light adaptation. This effect was greatest with red light and smallest with blue light. Between 39 and 78 ms, and only after bright light adaptation, we found higher GFP for blue, green, and white, when compared to red light. Hence, there seem to be two color dependent brain activation levels: an enhancement of red light after dim light adaptation, most likely caused by the predominant involvement of the cone system, and, after bright light adaptation, higher activations for blue than for red light, potentially mediated by the greater involvement of the melanopsin system.

Our first question was how dim and bright light adaptation impacts the response strength (GFP) to subsequent light stimuli. EEG responses for all light conditions were significantly higher after dim than bright light adaptation between 150 and 261 ms. This effect was surprisingly strongest for red light. Higher ERP responses (C1 component after 107 ms) were also found for red vs. blue checkerboards (Anllo-Vento et al., 1998), and in epileptic patients, where only red light elicited photo-convulsive seizures (Takahashi and Tsukahara, 1976). It is well known that the threshold of photoreceptors decreases in darkness (or in dim light as in our study), affecting rod and cone sensitivity with different time courses (Bartlett, 1965; Wong et al., 2005). Rods need about 20 to 40 min to fully adapt in darkness whereas cones adapt much faster; in the range of 5–10 min. The ipRGCs also adapt to darkness, (Do and Yau, 2013; Warren et al., 2003; Wong et al., 2005), but this dark adaptation is very slow: ipRGCs take up to 2 h to reach maximal light sensitivity (Fain et al., 2001). We propose that the strong GFP changes we found between dim and bright light adaptation from 150 to 261 ms (especially for red light), were predominantly caused by changes in cone sensitivity (and to a lower extent by ipRGCs) for two main reasons: 1) Rods and ipRGCs did not have...
time to reach their maximal light sensitivity level due to very slow light sensitivity gains during the dim light adaptation and 2) ipRGCs have minimal sensitivity for red light, compared to cones, and rods additionally very quickly became saturated when the light started to flash.

Why are light adaptation effects reflected in activity changes in frontal, temporal and occipital brain regions? Shared pathways between the rod/cone and the ipRGC system exist at the receptor level, where the activity of rod and cones is regulated by the ipRGCs (via dopaminergic amacrine cells) when ambient light changes (Zhang et al., 2008). There is also evidence for interactions between the two systems in more upstream neuronal pathways, e.g., in the lateral geniculate nuclei and the inter-geniculate leaflet of the primate brain (Dacey et al., 2005).

Therefore, any gain change at the retinal level leads to a change in higher networks of the brain, including primary and associated visual cortices. Since GFP was higher after dim light adaptation, there must be a functional link between dim light adaptation at the receptor level and adaptation at more upstream levels including higher sensitivity to light, because different brain regions were more activated after dim light adaptation.

Our second question was whether blue light exposure leads to less light adaptation than adaptation to other colors because of its alerting and activating nature, potentially mediated by the melanopsin system. We found that the presumably sustained tonic ipRGCs signaling after bright light adaptation in our study continued to be present and might attenuate (by unknown mechanism) light adaptation in a short early time range (39–78 ms). This lower adaptation was found for all colors which had greater effects on ipRGCs (i.e., which comprised more blue light), but not for red light.

Using electrical source imaging we found that the left middle frontal gyrus was the most likely brain source of the stronger responses to blue and green than to red light stimuli (between 39 and 78 ms). This implies involvement of cortical signaling pathways very early after light onset. One potential target region is the symmetrical frontal eye fields (FEF) in the middle frontal gyri. The FEF are known to control saccades and to convey very early retinal information signals to a variety of more downstream brain regions for executive, attentional and emotional processing (Pierrot-Deseilligny et al., 2004). It also shows fast activation after visual stimuli (O’Shea et al., 2004; Kirchner et al., 2009; Plomp...
et al., 2010). The FEF might therefore be a key structure for fast transla-
tion of non-visual responses to different brain regions. The fastest res-
ponse in cortical activity modulation during performance tasks has also
been observed in the left middle frontal gyrus within the first
minute of light exposure (Vandewalle et al., 2009), and in greater
P300 amplitudes of ERPs using an oddball task under monochromatic
blue light conditions (An et al., 2007).

A limitation of our study is that we investigated color and light adap-
tation effects with only one photon density. It would be very interesting
to apply the same ERP paradigm also to different irradiances of light,
and to further investigate brightness-related differences on fast EEG
brain responses. Secondly, we analyzed EEG responses in healthy
young adults. It would be important to test, whether fast EEG responses
to light of different colors are differently modulated in patients with
impaired vision, as well as in patients where ipRGC are known to be
less functional, for example in glaucoma patients. Thirdly, our study
design and our hypotheses were not aimed to test any light effects on
different opsins other than those of the three (ocular) photoreceptors.
The high artifact rejection rate (> 25% of the trials) most likely did not
influence our results, since the artifact exclusions were similarly distrib-
uted between conditions.

Our results indicate that at least two different mechanisms are
involved in event-related brain responses to colored light stimuli: 1) a ‘classical’ light adaptation process, with a lower brain excitability after
constant bright light and 2) an acute brain activation process which
counteracts the adaptation of EEG brain responses to blue, green and
white but not red light, after constant light exposure. To conclude, we
found strongest light adaptation effects in the GFP of the EEG with red
light, and least light adaptation effects with blue and green. Such com-
plex interactions between retinal light perception and brain responses
drive other physiological and behavioral responses to ambient light
changes.

Supplementary data to this article can be found online at http://dx.
do.org/10.1016/j.neuroimage.2014.06.071.

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