Brightness perception changes related to pupil size

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ABSTRACT

Dilating the pupils allow more quanta of light to impact the retina. Consequently, if one pupil is dilated with a pharmacological agent (Tropicamide), the brightness of a surface under observation should increase proportionally to the pupil dilation. Little is known about causal effects of changes in pupil size on perception of an object's brightness. In a psychophysical procedure of brightness adjustment and matching, we presented to one eye geometrical patterns with a central square (the reference pattern) that differed in physical brightness within backgrounds of constant luminance. Subsequently, with the other eye, participants (n = 30) adjusted to the same luminance a similar pattern (target) whose central square luminance was randomly set higher or lower in brightness than the reference. As only one eye was treated with Tropicamide, we assessed whether the subjective brightness of the target square shifted in a consistent direction when viewed with the dilated pupil compared to the untreated (control) eye. We found that, as the pupil increased post drug administration, so significantly did the sense of brightness of the pattern (i.e., higher brightness adjustments followed viewing the reference pattern with the treated (Tropicamide) eye). A reversed effect was observed when the control eye viewed the reference pattern first. The results confirm that even slight pupil dilations can result in an enhanced perceptual experience of brightness of the attended object, corresponding to an average increase of 2.09 cd/m² for each 1 mm increase in pupil diameter.

1. Introduction

There is inevitably a difference between measured and perceived levels of illumination. For example, a light bulb reduced to 10% of its maximum output will be perceived to be as 32%, or 3 times brighter, than the measured light's change (Rea, 2000). We surmise that even small changes in pupil diameters result in noticeable changes in the perceived luminous intensity of the external stimuli, as the aggregated amount of photons to fall on the retina each second is proportionate to the pupil area (Cornsweet, 1970). Hence, when the pupil widens, retinal illumination increases and presumably the object that one is currently directing gaze upon and actively attending to should also increase in intensity or brightness, while other properties (e.g., size or shape) should not change.

Research on the human perception of brightness has shown that the perceptual features of reflected light from objects are inherently confounded with the intensity of illumination (Adelson, 1993; Gilchrist, 1977; Purves et al., 2004; Zavagno, Daneyko & Liu, 2018). Given the continuous and immediate adjustments of the pupils, we need to consider how these changes in input may in turn affect the perception of light coming from an object. Surprisingly, little is known about causal effects of changes in pupil size on perception of an object’s brightness.

In achromatic perception, brightness can be defined as the 'perceived luminance' of an object related to the subjective sense of luminous intensity, not to the perceived reflectance of the object itself (Gilchrist, 2007). The brightness of a surface that is uniformly lit depends on the interaction between its reflectance and its level of illumination. In the case of luminous surfaces – as those displayed on a computer screen – brightness depends on the luminance output of the pixels that define the surface. However, other factors play a role in modulating brightness perception, such as the geometric layout of the scene (e.g. the contrast ratio at luminance edges, illumination or reflectance edges, etc.; e.g., Gilchrist, 1988, 2015; Zavagno, Daneyko & Sakurai, 2011). Thus, a gray surface may be any shade between black and white with various illumination levels specifying different brightness levels. Brightness may be strongly modulated by both edges and
luminance gradients (e.g. Soranzo et al., 2009; Zavagno & Daneyko, 2008). Given these facts, it is interesting to test how pupil size affects brightness perception and eventually interact with the type of contour defining a surface (e.g. sharp luminance change vs graded luminance change).

When general illumination levels change, the eye adapts to the background illumination to better distinguish objects over this background. Together with pupil changes, other adjustment mechanisms of visual adaptation operate, in part due to the bleaching of photopigments but also several neural transduction adjustments (Mansfield, 1976), which allow retinal adaptation to a changed level of background illumination to occur (Purves et al., 2001), over a period of few minutes, also while pupillary changes are controlled. In normal visual conditions, changing in pupils' size optimizes visual acuity at various levels of luminance (e.g., Campbell & Gregory, 1960; Campbell & Green, 1965; Campbell & Gubisch, 1966). The sphincter and dilator smooth muscles change the pupil aperture. The parasympathetic branch of the autonomic nervous system (ANS) controls the sphincter muscle and constriction of the pupil occurs when it is engaged. Dilation is largely driven by sympathetic ANS innervation of the dilator muscles (e.g., Barbur, 2004). Pharmacological agents like Tropicamide (a medication used to dilate the pupil during eye exams) result in pupil dilation to its maximal aperture within a period of about 45 min. This antimuscarinic drug blocks the receptors on the sphincter muscle and the accommodative ciliary muscle of the lens. The effect of Tropicamide is mydriasis and a more or less pronounced paralysis of accommodation (cycloplegia). Cycloplegia regresses faster than the mydriasis, which usually reaches its maximum within 46 min. Despite the marked local anticholinergic effect of Tropicamide, small movements of the pupil are still possible because of modulation of the sympathetic innervation of the dilator muscle and modulation of the central sympathetic innervation inhibiting the Edinger-Westphal nucleus. A pupil pharmacologically dilated by an anticholinergic agent may even constrict considerably if the sympathetic tone is reduced in sleep (see Krastel et al., 1996). However, this could not be expected during this experiment where the participants were forced to stay concentrated and alert.

Early studies of the effect of pupillary size on visual acuity also used atropine agents to dilate pupils fully, but then tested vision through artificial pupils. In a seminal article, Campbell and Gregory (1960) used sinusoidal gratings (i.e. striped patterns) to measure at which luminance level the stripes remained visible for participants with maximum dilated pupils employing atropine as the dilating agent. In the second part of the experiment, the perception task was performed while viewing the patterns through an artificial “pupil” of adjustable size. Although this method allowed for systematic control of the amount of light stimulating the pupil, it is difficult to generalize these results to a situation with a natural moving pupil since the experimental situation is closer to looking into a peep hole of variable sizes, rather than looking at a visual scene with a different pupil diameter.

In the current study, instead of using an artificial pupil, we chose a monocular dilation method and measured luminance adjustments while the pupil aperture pharmacologically dilated. We monitored pupil size changes of both the treated and untreated eye with an infrared eyetracker between experimental blocks to relate the degree of pupil dilation to possible changes in brightness perception using an interocular comparison method. The experiments contained both high contrast black and graded cruciform patterns (see Fig. 1B) to vary the luminance boundaries (Gilchrist, 2015) and potentially, the perceived brightness of the surface. However, any increase of the diameter of the pupil may be accompanied by retinal adaptation to changed luminance. One possibility is that these visual adaptation mechanisms may result, over some time, in a normalization of brightness, also to avoid dazzling effects from high luminance levels. Hence, it is an empirical question – given retinal adaptation – whether the pupil under the effect of Tropicamide will experience a measurable increase in an object's brightness.

Specifically, using an interocular design, we alternately tested either eye, Tropicamide versus control eye, while masking the other eye. In this manner, we were able to relate the gradually increasing pupillary dilation in the Tropicamide eye to brightness perception. Specifically, participants viewed with the Tropicamide eye a central reference square (differing in brightness from trial to trial; see Fig. 1A). Then the Tropicamide eye was covered and the participant adjusted the luminance of a central target square while looking at it with the control eye to match its brightness to that of the reference square.

We expected that, with an increase in dilation of the Tropicamide-treated eye, 1) brightness perception would increase, as indicated by the brightness matching procedure. Therefore, 2) when the target square was viewed by the Tropicamide eye, it would be adjusted to be relatively darker than the reference square seen just before with the control eye. In addition, 3) such a pupil-related brightness enhancement was expected to increase and decrease over time since the pupil will first dilate to a near maximal level and then tend to decrease again. Finally, 4) as shown in several studies (Binda, Pereverzeva, & Murray, 2013; Laeng & Endestad, 2012; Naber & Nakayama, 2013; Zavagno, Tommasi, & Laeng, 2017), luminance gradients converging to the center of patterns can induce “illusory glare” (e.g. Zavagno & Daneyko, 2017) or a ‘halo effect’ of luminosity (when diverging), in particular with the lighter gray (Kobayashi, Matsushita & Morikawa, 2018). This illusory glare yields a subjective increased brightness of a stimulus, which correlates to a top-down constriction of the pupil. Because illusory glare may cause two stimuli of identical physical brightness to be perceived differently from each other, the glare (or gradient) stimuli should be judged as brighter in the adjustment task.

2. Materials and methods

2.1. Participants

Thirty healthy participants (14 females, ages 18–47, mean age = 25 years; SD = 6.89) with normal vision were recruited at the University of Oslo. The participants were treated according to the declaration of Helsinki (1964) and the study was approved (No. 2011/1337) by the Regional Ethical Committee of Southeast Norway. All participants signed a written informed consent form.

2.2. Materials

Stimuli consisted of two cruciform patterns, one with sharp changes in the central square’s boundaries, dubbed ‘black’ and one cruciform with gradient boundaries (see Fig. 1). The cruciform patterns’ center squares varied between 61.46 and 117.61 cd/m² in luminance. In a trial, the initially seen center square was nonadjustable and varied randomly from trial to trial, either 10 units up or down within the selected 61.46–117.61 cd/m² range. The subsequently seen target square’s brightness also varied randomly in brightness, but 33% of the time it was either lower in luminance than the reference, higher, or equal. This second target square was manually adjustable in luminance by using arrows on the keyboard and the task was to match it in brightness with the previously seen target with the other eye. Whether the cruciform patterns in each trial appeared either with black contours or with gradients also varied at random. All figures were generated and run in Matlab R2017a (Mathworks) using the Psychophysics Toolbox (Brainard, 1997) and the cruciform patterns were always presented against the same uniform gray background, set at 38.61 cd/m².

We used a 1% pharmaceutical Tropicamide eye drop to dilate one of the participants’ pupils. The expected dilating effect occurs typically within 40 min, and may last up to 24 h before completely returning to the original resting-state. Because the effect of Tropicamide may work slower on brown eyes than blue eyes (e.g. Ogun, et al., 2014, but see Richardson, 1982), we registered each of the participants’ eye color.

A Dell LCD monitor (calibrated using Spyder 4 Elite) and a SMI RED

500 infrared eye-tracking device (SensoMotoric Instruments®, Germany), with a display resolution of 1680 × 1050 pixels and a resolution of eye position that is greater than 0.1°, with a minimum gaze point accuracy of 0.5°, was used. During eye tracking, participants simply viewed a sequence of screens that consisted of three gray backgrounds with values of 32.38, 38.61 and 45.61 cd/m², and the sequence changed every 10 s. The background contained a central unfilled circle (size = 8.5°) with a circumference of a darker shade of gray (26.11 cd/m²).

2.3. Procedure

At the start of the experiment, participants were seated 60 cm from the screen. A standard 4-point calibration procedure was conducted, followed by a baseline or resting-state measure of the pupil size right before Tropicamide was administered. All pupil measurements (including baseline) consisted of the gray screen sequence that lasted 10 s for each screen over a 30 s duration. All participants were instructed to keep their gaze inside the central circle. By maintaining gaze onto a central position, while the head was stabilized with a chinrest we aimed to reduce artifacts in pupil measurement with gaze and head movement that are common with most infrared eye-trackers (Sirois & Brisson, 2014). The eye-tracking data were recorded at a rate of 60 Hz.

After calibration, participants began a practice block to learn the trial setup. The practice block consisted of 5 trials, after which the participant’s dominant eye was assessed using the Miles test (Miles, 1929, 1930). A Tropicamide eye drop was delivered alternately to the participants’ dominant/subdominant eye. Each participant then put on ophthalmology test glasses that allowed either eye to be covered by a removable opaque screen.

Throughout the tasks, an identical matching procedure was used. First, one eye was covered and a cruciform pattern was viewed for 4 s with the Tropicamide/Control eye, and the participant was instructed to focus attention on its central square (from here on ‘reference square’) and try to remember the brightness of the reference square. The participant’s uncovered eye was then covered, and the previously covered eye was uncovered and by pressing the keyboards’ “space bar”, a new cruciform pattern appeared on screen. The participant was instructed to adjust the brightness of the new pattern’s central square (from here on ‘target square’) using the up/down arrow keys on the keyboard, until reaching the ‘same’ brightness level of the reference square previously viewed with the current covered eye. Each arrow key press changed the cd/m² by 0.002 units in the direction indicated by the key (higher, lower). When participants judged the brightness of the target square to be equal to the reference square, they pressed the space bar, the eye-cover was switched, and the next trial commenced. The experimenter switched the eye-cover throughout the experiment to make sure that the participant would see the reference – and target squares with only one eye and in the correct sequence.

The experiment consisted of 8 blocks with 12 trials. Within the 8 blocks half of the trials contained black cruciform patterns, the other half had gradient cruciform patterns. The type of pattern to be seen was randomly selected. Half of the time, participants viewed the reference square with the Tropicamide eye, and half of the time with the Control eye. After each block, which was approximately 5 min in total, the participants had their pupil size recorded using the infrared eye-tracker. A total of 9 pupil recordings (including the initial resting-state baseline) were made. The experiment lasted approximately one hour and all participants were remunerated for their participation (300 NOK).

By subtracting the target cd/m² from the matched cd/m², we created a difference variable called Luminance Change, and separately computed these scores for the ‘black’ cruciform patterns and the ‘gradient’ cruciform patterns during the 8 blocks.

Analyses were done in SPSS Statistics 25. For the linear regression, the last two blocks (7 and 8) were excluded as the treated pupil had started to constrict and returning to normal. All pupil sizes are displayed in mm and luminance is displayed in cd/m².

3. Results

A preliminary repeated-measures ANOVA on Luminance Change showed that there was no significant differences in luminance matching due to Gender (female, male), F(8, 17) = 0.19, p = .99, or Eye Color (blue, green, brown) F(16, 34) = 0.70, p = .78, hence, we removed these factors for all subsequent analyses.

3.1. Pupil size

To confirm the pharmacological effects on the pupil of the Tropicamide eye compared to the Control eye, a repeated measures...
3.2. Target’s luminance change

As expected, a repeated measures ANOVA showed a main effect of Pupil (Tropicamide Eye: \( M = -8.58, SD = 12.83 \), Control Eye: \( M = 3.15, SD = 17.88 \)) \( F(1, 29) = 32.34, p < .001, \eta^2_p = 0.53 \), Cruciform patterns \( F(1, 29) = 4.22, p < .05, \eta^2_p = 0.13 \) and Blocks \( F(7, 23) = 2.74, p = .03, \eta^2_p = 0.46 \), on Luminance Change. There was also a significant interaction effect of Pupil and Cruciform Pattern (Black, Gradient) \( F(1, 29) = 10.46, p = .003, \eta^2_p = 0.27 \), as well as Pupil and Blocks \( F(7, 23) = 6.29, p < .001, \eta^2_p = 0.66 \) (see Fig. 2B). The interaction effect between Pupil, Cruciform Pattern and Blocks \( F(7, 23) = 4.78, p = .002, \eta^2_p = 0.59 \) was also significant. As Fig. 2 illustrates, the above effects were due to different adjustments of the target’s luminance, in the expected directions, dependent on whether the reference was first seen by the either the tropicamide or control eye as well as whether the stimuli consisted of either the black or gradient cruciform patterns.

A paired samples \( t \)-test showed that there were significant differences in Luminance Change of Black figures between Tropicamide Eye and Control Eye in all blocks except the first block (see Table 2). As can also be seen in Table 2, the Luminance Change of Gradient cruciform patterns became significantly different after 4 blocks.

A separate repeated-measures ANOVA was used to explore the effect of the stimulus when the target’s luminance was adjusted with the Tropicamide eye. This showed that there was no significant difference between Cruciform Patterns (gradient, black) \( F(1, 29) = 1.83, p = .19, \eta^2_p = 0.06 \), but a difference emerged over Blocks \( F(7, 23) = 3.33, p = .013, \eta^2_p = 0.50 \) and between Cruciform Patterns and Blocks \( F(7, 23) = 8.40, p < .001, \eta^2_p = 0.72 \). However, paired \( t \)-tests revealed that the only significant difference occurred in Block 3 (mean difference = 13.76, \( SD = 10.53 \)), \( t(29) = 7.15, p < .001 \) (see Fig. 4). A closer inspection of these data showed that the gradient pattern in block 3 – as seen with Tropicamide eye – had approximately half the trials of the other blocks and patterns. We believe that the reason for this asynchrony might be simply due to chance, given that we applied a fully randomized sequence of trials per condition in the whole experiment. Consequently, the target squares’ initial brightness could vary upwards 63% of the time in this particular condition, and presumably this spurious ‘systematicity’ made it function as an anchor, which could account for this flawed result. In fact, a look at Figs. 3 and 4 reveal a continuous, smooth, change in pupil sizes, consistent with the slow acting effect of the drug over time.

Instead, when the target’s luminance was adjusted by the Control eye, there was a significant difference between Cruciform patterns \( F(1, 29) = 11.25, p = .002, \eta^2_p = 0.28 \), and Blocks \( F(7, 23) = 5.41, p = .001, \eta^2_p = 0.62 \), but no interactive effect between Cruciform patterns and Blocks \( F(7, 23) = 0.98, p = .47, \eta^2_p = 0.23 \) (see Fig. 3). A paired \( t \)-test revealed differences in several Blocks, namely: Block 3 (mean difference 10.47, \( SD = 24.01 \)), \( t(29) = 2.39, p = .024, \) Block 5 (mean difference 14.13, \( SD = 22.34 \)), \( t(29) = 3.47, p = .002, \) Block 6 (mean difference 9.52, \( SD = 19.49 \)), \( t(29) = 2.69, p = .012 \) and Block 8

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Table 1

<table>
<thead>
<tr>
<th>Pupil size</th>
<th>Control eye</th>
<th>Tropicamide eye</th>
<th>Mean difference</th>
<th>( t(29) )</th>
<th>( P )</th>
<th>Cohens ( d )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pretreatment</td>
<td>4.80 (0.74)</td>
<td>4.82 (0.76)</td>
<td>0.02 (0.22)</td>
<td>0.61</td>
<td>.54</td>
<td>0.02</td>
</tr>
<tr>
<td>After block 1</td>
<td>4.19 (0.62)</td>
<td>6.53 (0.92)</td>
<td>2.35 (0.95)</td>
<td>13.57</td>
<td>&lt; .001</td>
<td>2.95</td>
</tr>
<tr>
<td>After block 2</td>
<td>3.98 (0.65)</td>
<td>7.30 (0.82)</td>
<td>3.32 (0.92)</td>
<td>19.71</td>
<td>&lt; .001</td>
<td>4.69</td>
</tr>
<tr>
<td>After block 3</td>
<td>3.79 (0.54)</td>
<td>7.51 (0.76)</td>
<td>3.72 (0.85)</td>
<td>24.10</td>
<td>&lt; .001</td>
<td>5.60</td>
</tr>
<tr>
<td>After block 4</td>
<td>3.70 (0.50)</td>
<td>7.72 (0.69)</td>
<td>4.02 (0.71)</td>
<td>31.31</td>
<td>&lt; .001</td>
<td>6.60</td>
</tr>
<tr>
<td>After block 5</td>
<td>3.66 (0.48)</td>
<td>7.72 (0.69)</td>
<td>4.06 (0.71)</td>
<td>31.24</td>
<td>&lt; .001</td>
<td>6.75</td>
</tr>
<tr>
<td>After block 6</td>
<td>3.65 (0.47)</td>
<td>7.68 (0.65)</td>
<td>4.04 (0.67)</td>
<td>33.04</td>
<td>&lt; .001</td>
<td>7.09</td>
</tr>
<tr>
<td>After block 7</td>
<td>3.65 (0.43)</td>
<td>7.77 (0.62)</td>
<td>4.12 (0.67)</td>
<td>33.48</td>
<td>&lt; .001</td>
<td>7.68</td>
</tr>
<tr>
<td>After block 8</td>
<td>3.65 (0.43)</td>
<td>7.12 (0.62)</td>
<td>3.47 (0.72)</td>
<td>26.32</td>
<td>&lt; .001</td>
<td>6.45</td>
</tr>
</tbody>
</table>
Table 2
Luminance of cruciforms. Mean luminance change (cd/m²) as adjusted by Control eye and Tropicamide Eye, and the mean difference in mean luminance change in black and gradient cruciform patterns between eyes in each block (SDs in parentheses).

<table>
<thead>
<tr>
<th></th>
<th>Control eye</th>
<th>Tropicamide eye</th>
<th>Mean difference</th>
<th>t(29)</th>
<th>p</th>
<th>Cohens d</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black cruciform</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Block 1</td>
<td>−1.05 (16.62)</td>
<td>−5.11 (15.11)</td>
<td>4.06 (22.46)</td>
<td>0.99</td>
<td>0.33</td>
<td>0.17</td>
</tr>
<tr>
<td>Block 2</td>
<td>−2.73 (21.80)</td>
<td>−8.20 (16.22)</td>
<td>10.93 (25.32)</td>
<td>2.36</td>
<td>0.02</td>
<td>0.19</td>
</tr>
<tr>
<td>Block 3</td>
<td>9.10 (15.49)</td>
<td>−14.20 (8.10)</td>
<td>23.31 (16.68)</td>
<td>6.83</td>
<td>&lt;0.001</td>
<td>1.12</td>
</tr>
<tr>
<td>Block 4</td>
<td>8.16 (18.40)</td>
<td>−10.21 (12.55)</td>
<td>18.36 (25.20)</td>
<td>3.99</td>
<td>&lt;0.001</td>
<td>0.84</td>
</tr>
<tr>
<td>Block 5</td>
<td>11.78 (20.15)</td>
<td>−10.07 (19.60)</td>
<td>21.85 (36.57)</td>
<td>3.27</td>
<td>0.003</td>
<td>1.38</td>
</tr>
<tr>
<td>Block 6</td>
<td>11.60 (19.13)</td>
<td>−14.32 (13.67)</td>
<td>25.93 (27.90)</td>
<td>5.09</td>
<td>&lt;0.001</td>
<td>1.27</td>
</tr>
<tr>
<td>Block 7</td>
<td>6.70 (16.61)</td>
<td>−7.80 (12.29)</td>
<td>14.50 (21.81)</td>
<td>3.64</td>
<td>0.001</td>
<td>0.66</td>
</tr>
<tr>
<td>Block 8</td>
<td>10.90 (20.04)</td>
<td>−8.32 (10.26)</td>
<td>19.22 (25.76)</td>
<td>4.09</td>
<td>&lt;0.001</td>
<td>0.86</td>
</tr>
<tr>
<td>Gradient cruciform</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Block 1</td>
<td>−11.98 (24.80)</td>
<td>−4.56 (13.39)</td>
<td>−7.42 (31.74)</td>
<td>−1.28</td>
<td>0.21</td>
<td>0.26</td>
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<tr>
<td>Block 2</td>
<td>−3.19 (19.69)</td>
<td>−11.61 (21.93)</td>
<td>8.41 (34.09)</td>
<td>1.35</td>
<td>0.19</td>
<td>0.37</td>
</tr>
<tr>
<td>Block 3</td>
<td>−1.37 (20.36)</td>
<td>−0.44 (7.08)</td>
<td>−0.93 (24.40)</td>
<td>−0.21</td>
<td>0.63</td>
<td>0.84</td>
</tr>
<tr>
<td>Block 4</td>
<td>1.10 (18.15)</td>
<td>−6.18 (14.21)</td>
<td>7.27 (24.63)</td>
<td>1.62</td>
<td>0.12</td>
<td>0.31</td>
</tr>
<tr>
<td>Block 5</td>
<td>−2.35 (16.15)</td>
<td>−9.61 (9.74)</td>
<td>7.26 (15.44)</td>
<td>2.58</td>
<td>0.015</td>
<td>0.40</td>
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<tr>
<td>Block 6</td>
<td>2.03 (11.73)</td>
<td>−9.75 (10.18)</td>
<td>11.78 (14.99)</td>
<td>4.30</td>
<td>&lt;0.001</td>
<td>0.74</td>
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<td>Block 7</td>
<td>4.63 (18.25)</td>
<td>−10.98 (14.05)</td>
<td>15.60 (24.80)</td>
<td>3.45</td>
<td>0.002</td>
<td>0.66</td>
</tr>
<tr>
<td>Block 8</td>
<td>1.69 (8.74)</td>
<td>−5.84 (5.87)</td>
<td>7.53 (9.78)</td>
<td>4.22</td>
<td>&lt;0.001</td>
<td>0.66</td>
</tr>
</tbody>
</table>

Fig. 3. Effect of cruciform patterns on each eye. A) Mean luminance change (cd/m²) of the Black and Gradient cruciform patterns over blocks adjusted with the Control eye and, B) adjusted with the Tropicamide eye. Error bars represent SE.

(mean difference 9.21, SD = 22.30), t(29) = 2.62, p = .03, indicating that the luminance of the Black cruciform patterns tended to be adjusted brighter than the Gradient cruciform patterns.

We also conducted a linear regression on Luminance Change of the target adjusted with Tropicamide eye and its pupil size (over the first 6 blocks). The regression was significant, F(1,178) = 7.65, p = .006 (see Fig. 4) and revealed a luminance setting decrease of −2.09 cd/m² (SD = 0.80) by each increase in 1 pupil mm of the eye seeing the reference pattern (see Fig. 4A). A similar linear regression of Luminance Change of the target adjusted with Control eye showed an increase by 1.58 cd/m² (SD = 1.11) by each increase in 1 pupil mm of the pupil size of Tropicamide eye when viewing the reference pattern (see Fig. 4). However, this regression failed to reach statistical significance, F (1,178) = 2.04, p = .15.
4. Discussion

We hypothesized that brightness would be enhanced by an enlargement of the pupil. In this study, brightness enhancement was shown through darker matching of the target by the Tropicamide eye. In other words, because the target square seen by the Tropicamide eye appeared brighter than the reference square seen by the control eye, the participants adjusted the brightness of the target square down below the brightness of the reference square to match the lower levels of brightness perceived by the control eye. The measured “decrease” in brightness equaled an average increase in perceived brightness by the Tropicamide eye of 2.09 cd/m² of pixels’ brightness for each 1 mm increase in pupil diameter. Instead, when the reference square was viewed with the Tropicamide eye, the adjustment of the target square’s luminance made with the control eye yielded a luminance increase of 1.58 units of pixels’ luminance for every 1 mm of pupil dilation (in the Tropicamide eye). In addition, the brightness change either increased or decreased over blocks in correspondence with the dilation of the treated pupil. Interestingly, in a recent experiment (Laeng et al., 2018) on the Face Race Luminance illusion (Levin & Banaji, 2006), it was found that participants’ perception of luminance-matched faces as darker/lighter than one another was associated with no more than a 2% difference in pupil diameters, equivalent to just a 3.3% change of the pupil’s area.

Retinal adaptation to brightness may concomitantly reduce brightness, as a large pupil may also cause the retina to adapt to the greater brightness, which could reduce or normalize brightness perception. Interestingly, when the pupils were largest, in block 4 and 5, the brightness perception was slightly reduced when adjusted with the Tropicamide eye (see Fig. 3B). It is possible that such a reduction in mean luminance change of the black cruciform patterns (in blocks 4 and 5), of approximately 4 cd/m², may reflect a process of retinal adaptation to the greater brightness since the effect of tropicamide is supposed to last well beyond the time window of testing used in the present experiment. Visual adaptation may be visible also in blocks 7 and 8, as the Tropicamide eye is still over 7 mm, while the brightness seems further reduced, which appears most clearly with the black cruciform patterns.

Contrary to predictions, we did not find any enhanced effects of illusory glare in the brightness adjustment task, as it appears that the black cruciform patterns induced more brightness compared to the gradient cruciform pattern when adjustments were made using the control eye (as the reference square was seen with the Tropicamide eye; Fig. 4A). When adjusting with Tropicamide eye to the reference square seen with the control eye, there were no differences between black and graded cruciform (except in block 3). As the reference squares in this study varied between 26.11 and 117.61 cd/m², we surmise that the reference squares may not have been sufficiently bright to yield a glare effect. As even 117.61 cd/m² was darker than the surrounding gradient edges, this may have caused an apparent clear-cut edge against the inner white of the gradient, causing the reference square to appear darker than it was. In fact, the current results suggest that the reference squares were perceived as considerably brighter during viewing of black vs gradient cruciform patterns with the Tropicamide eye. Thus, the sharp contrast of the dark edges seems to have increased the perceived brightness, while the lighter edges did not.

We did not measure the pupil response to gradients in this experiment, but previous studies using similar cruciform stimuli did reveal a constriction of the pupil to illusory glare (Zavagno, Tommasi, & Laeng, 2017). In addition, a recent experiment shows that observers who show pupil constrictions to illusory glare stimuli with converging gradients also tend to subjectively perceive them as brighter than their inside-out versions (Suzuki, Minami, Laeng, & Nakauchi, 2019). Interestingly, another recent study found greater pupil constrictions to red and blue light when the pupil was diluted with Tropicamid and phenylephrine hydrochloride compared to normal sized pupils (Ba-Ali, et al., 2018). Hence, the subjective interpretation of more intense light, after forced dilation, could yield a stronger pupillary light reflex-like response.

In addition, we did not test pupillary function during screening for this study and our oldest participant was 47 years old, at an age where near vision has often started to decline. This particular participant did not use glasses and reported no problems refocusing from far away to close objects. In future studies it may be best to recruit only participants under the age of 40 to avoid possible accommodation problems. Also, we did not test the participants’ brightness perception of each eye before pharmacological treatment. We cannot exclude that there may be some interocular differences in brightness perception amongst healthy people.

A caveat in using Tropicamide during visual matching experiments is that it may cause blurry vision, as Tropicamide produce mydriasis and cycloplegia that could both reduce visual acuity and accommodation, making it harder to focus on near stimuli. However, Montgomery & Macewan (1989) found that one drop of Tropicamide at 1% caused little disturbance on visual acuity and accommodation.

Future studies could also monitor the pupils during viewing of and matching of the stimuli, instead of between blocks, to further address the question of whether the pupillary light reflex in the non-dilated eye is enhanced during the viewing of graded versus black cruciform with the dilated eye. In addition, pseudo-randomization could be used to ensure that all conditions get an equal number of trials. Finally, it would be interesting to test whether pupil size also affects the perception of achromatic surface color. Given that within a certain range of illumination variations, lightness has proved to be quite constant within specific simultaneous lightness contrast displays with cross-like patterns similar to those employed in our experiment (Zavagno, Daneysko & Liu, 2018).

In conclusion, as the eye’s pupil increases so does a person’s sense of brightness of the target, as indicated by the degree of adjustments made while viewing with the treated or untreated eye. Even a slight dilation of the pupil results in an increased perceptual experience of brightness of the attended object.

CRediT authorship contribution statement

Unni Sulutvedt: Conceptualization, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. Daniele Zavagno: Conceptualization, Writing - review & editing. Jamie Lubell: Software, Writing - review & editing. Siri Leknes: Writing - review & editing. Sigrid A. Rodez Benavent: Resources, Writing - review & editing. Bruno Laeng: Conceptualization, Supervision, Methodology, Writing - original draft, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.visres.2020.09.004.

References
