The Effects of Psychosensory Pupil Responses and Color on Detection Performance in a

Light and Dark Environment

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Abstract

The aim of this study was to investigate the effect of psychosensory pupil size responses and color on detection performance in a light and dark environment, to examine a possible shift from rod-dominated vision to cone-dominated vision. A total of 55 participants, of which 43 participants participated in the light condition (31 females, 12 males, Mage = 20.51, SD = 2.21) and 50 in the dark condition (35 female, 15 males, Mage = 20.52, SD = 2.23), took part in this experiment. We measured the pupil size prior to the presentation of a stimulus during a cognitive task. We found that the psychosensory pupil size in the detection task has a significant effect on detection accuracy, where big pupil size resulted in better detection accuracy. In addition, we found an effect of color on the detection of faint stimuli, where red targets resulted in a higher detection accuracy than blue targets, with this difference reaching statistical significance only in the lighting condition. No interaction effect was found between pupil size and color on detection accuracy. Our findings suggest a complex interaction between pupil dynamics and color sensitivity, warranting further investigation into the underlying mechanisms and conditions that influence visual processing and perception.

Keywords: psychosensory pupil size, detection

The effects of Psychosensory Pupil Responses and Color on Detection Performance in a Light and Dark Environment

Perception is the way one receives and processes sensory information. This process relies for a large part on visual processing within the eye. The dilation of the pupil plays a central role in this process. Pupil size shapes visual processing by determining the amount of light that enters the eye, as well as how that light is focused. Research on pupil size has shown that it does not just react to light known as the pupil light reflex, (Ellis, 1981; Kankipati et al., 2010), but also responds to cognitive activity (Fietz et al., 2021; Granholm & Steinhauer, 2004). Despite the extensive research on the causes of these cognitively induced pupil size changes, there is a lot more to find out about how this process happens and what effects it has.

Variations in pupil size offer a distinctive insight into brain activity. The measuring of the pupil size, known as pupillometry, therefore has been a prominent topic within the research of cognitive psychology. Cognitive pupillometry methods differ widely across different types of studies, from task-evoked measurements to baseline measurements (Mathôt & Vilotijević, 2022). In the current study we will be measuring spontaneous pupil size fluctuations, by measuring the different pupil sizes prior to the presentation of a stimulus during a cognitive task.

When the size of the pupil changes because of cognitive causes, we refer to this here as psychosensory pupil size changes. These psychosensory pupil size changes indicate the differences in pupil sizes that are not caused by changes in luminary levels and are thereby induced by internal factors rather than external factors. For example, the amount of pupil dilation does not always match the actual decrease of brightness levels, portraying a difference between perceived brightness and actual brightness (Sulutvedt et al., 2021). Psychosensory pupil size changes can be caused by different reasons, such as an increased state of arousal or attention, but also by cognitive effort. For example, spontaneous pupil

dilations were found to be related to activation of the salience network, thalamus, and frontoparietal regions (Bradley et al., 2008; Eckstein et al., 2017; Schneider et al., 2016). In another study an increase in pupil dilation was associated with a high visual working memory load (Stolte et al., 2020). Furthermore, pupil size changes caused by cognitive factors were found to be strongly associated with activation of the locus coeruleus. Activation of the locus coeruleus consistently predicts changes in the size of the pupil (Joshi et al., 2016; Murphy et al., 2011).

Pupil size changes are known to influence visual sensitivity and acuity. When pupils are large, they allow more light to enter on the retina resulting in better visual sensitivity (Eberhardt et al., 2021). When pupils are small, they allow for less light to enter the eye which leads to sharper vision and focus of incoming light on the fovea, where visual acuity is the highest (Campbell & Gregory, 1960; Ebitz & Moore, 2019). If we manipulate pupil size through peripheral brightness in discrimination and detection tasks, we see that reduced pupil size enhances the ability to discriminate subtle stimuli, whereas increased pupil size improves the detection of faint stimuli (Mathôt & Ivanov, 2019). Additionally, overall pupil size is larger during detection tasks than during discrimination tasks, suggesting an automatically adjusted pupil size based on the type of task presented.

It has recently been discovered in a study on pupil size and color sensitivity that a relation exists between psychosensory pupil size and the activation of rod-dominated and cone-dominated vision in mice (Franke et al., 2022). It was shown that during an active cognitive state resulting in pupil dilation, a dynamic shift in color sensitivity appeared. It was found that when the mice were looking at colored scenes and were active, certain parts of their cortex became more sensitive to different kinds of lights, such as ultraviolet light opposed to green light. This happened because their pupils dilated during the active state, which made their eyes switch from using rod-type cells to cone-type cells. This switch in

photoreceptor activity also occurred when there were no changes in behavioral state, which suggests that pupil dilation alone was sufficient to induce this effect.

Cone type cells are responsible for color vision and are typically active during bright lighting conditions because they need more light to be activated (Ebrey & Koutalos, 2001). They consist of three different types: the long-wave (L) cones, medium-wave (M) cones and the short-wave (S) cones. Red light consists of long wavelengths, thus triggers the L-cones, green light consists of medium wavelengths, thus triggers M-cones and (Dacey, 1999; Yoshioka et al., 1996) and blue light consists of short wavelengths, thus triggers S-cones. Additionally, L- and M-cones become absent in the periphery of the human retina (Mullen et al., 2005). Rods are often active during dim lighting conditions because they are more sensitive to light, thus need less light to be activated (Ingram et al, 2016). They are known to be less responsive to color than cones. They have however shown to be sensitive to the color blue. They display an absorption peak around 500 mµ, which means they are able to absorb blue wavelengths (Bowmaker & Dartnall, 1980; Brown & Wald, 1964b; Reitner et al., 1991).

Several other factors are known to have an effect on pupil size and detection performance as well. First of all, commonly used pharmacological stimulants are shown to affect pupil size and attention. Nicotine is shown to cause pupil constriction and to improve attention and cognitive performance in some studies (Levin et al., 1998; Lie & Domino, 1999; Wardhani et al., 2020). Other stimulants that have been found to cause inconsistent pupillary activity are alcohol (Castro et al., 2014) and caffeine (Bardak et al., 2016; Wilhelm et al., 2013). Lastly, the amount of sleep, especially sleep deprivation, can lead to pupil size instability (Van Egroo et al., 2019; Wilhelm et al., 1998).

In this research, we investigate whether the detection of targets in the visual field varies based on the colors of the targets and explore the relationship between psychosensory pupil size and this detection process. Additionally, we conduct a control analysis examining

the potential impact of nicotine consumption on these perceptual mechanisms. If a color advantage in small or large pupil size exists, this could give us more information on how psychosensory induced pupil size affects color detection and the possible activation of rod and cone type cells. We use a detection task where differently colored dim targets are presented across the visual field. The targets are either blue or red and located from parafoveal to peripheral areas. During the experiment pupil size is measured continuously, after which we analyze the data prior to the presentation of each target. There are two experimental settings, one where participants undergo a dark adaptation procedure prior to doing the experiment and perform the task in a dim environment, and one where they do not undergo dark adaptation and perform the task in a light environment. To exclude external factors from our research we included a control analysis for nicotine, alcohol and caffeine consumption and sleep deprivation, by having the participants fill in a questionnaire. Our goal is to determine whether the results of previous studies on psychosensory pupil size, detection and color sensitivity are replicable.

We expect an overall large pupil advantage, where targets are better detected when pupils are bigger than when they are smaller prior to target presentation, due to more light being let in on the retina resulting in better visual sensitivity in bigger pupils. Additionally, we expect the detection of blue targets to be less impaired by small pupil size compared to the detection of red targets, given that rods are expected to be activated during small pupil size which can detect blue light.

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Method

Participants

A total of 55 participants, of which 43 participants in the light condition (31 females, 12 males, $M_{age} = 20.51$, SD = 2.21) and 50 participants in the dark condition (35 females, 15 males, $M_{age} = 20.52$, SD = 2.23), took part in this study. These numbers differ because some participants only showed up for one of the two sessions. All participants were psychology students at the University of Groningen. All participants had normal to corrected vision and normal color vision. The participants were asked to remove any eye make-up before the experiment. Participants were given partial course-credit as an inducement to participate in the study. On the basis of criteria developed by the EC-BSS at the University of Groningen, the study was exempt from full ethical review. The study was given the code PSY-2324-S-0311 by the EC committee. After pre-processing, 8 participants from the light condition and 5 participants from the dark condition were excluded from the initial data due to missing or default data.

Materials & Software

Software and Hardware

In this study, the monitor on which the detection task was presented was an Iiyama Prolite G2773HS, with model number PL2773H and featuring a Full HD 1080p resolution at 1920 x 1080 pixels (2.1 megapixels). The monitor boasted a refresh rate of 100 Hz. Pupil size was recorded using the Gazepoint eye-tracker with a sampling rate of 60 Hz. The experimental software employed to take the baseline measurement and detection task was OpenSesame, version 4.0.13, developed by Mathôt et al. (2012). A headrest was used to ensure stability. Luminance of the background of the screen was set at 4.83 cd/m2 during the baseline measurement and at 0.20 cd/m2 during the detection task. The color of the background was shown in HEX color format #3d3846 during the baseline measurements and in #000000 during the detection task.

Stimuli

The opacity of the targets was set at 0.30% for red targets and at 0.40% for blue targets, with a slightly higher opacity for blue targets than red targets at the authors discretion to compensate for the fact that red targets are easier to detect on a dark background. In the first three blocks, consisting of 56 trials each, a staircase method was used, where the opacity decreased when the right response was given three times in a row, and increased when one wrong response was given. This was used to find each participant's individual detection threshold. The targets' onset was randomly decided between 1000 and 2000 milliseconds. The presentation of the target lasted for 50 milliseconds, whereafter the trial continued for another 1500 milliseconds. This resulted in a total trial length between 2500 and 3500 milliseconds.

Targets were presented as faint luminant patches in HEX color format, with red designated as #FF0000 and blue as #0000FF. The size of the targets was adjusted based on their distance from the fixation point to account for cortical magnification. The formula used to calculate this was:

$$size = \frac{px_per_degree \times size}{(1+0.42 \times ecc + 0.0001 \times ecc^3)^{-1}}$$

In this formula, px_per_degree is the pixels per degree of visual angle, which is 34, size is the size of the stimulus in pixels and ecc is the eccentricity of the stimulus in pixels. The sizes varied between 21 pixels and 103 pixels, with eccentricities of 20 and 400 pixels, and visual angles of 0.50 and 2.47 degrees. The luminance of the red targets was 33.59 cd/m2 at full contrast and of the blue targets 12.34 cd/m2 at full contrast. The fixation dot was presented alternating from a square to a circle whenever a response was given, with a diameter of 15 pixels. The targets were randomly presented on different eccentricities over the screen, differing from near the fixation dot with a minimum eccentricity of 20 pixels to

further away from the fixation dot with a maximum eccentricity of 400 pixels. See Figure 1

for an illustration of the target presentation.

Figure 1

Illustration of Red Target and Fixation Dot on Background



Questionnaires

We used two questionnaires in this study. The first questionnaire contained questions about the demographics of the participants. In this questionnaire they were asked about their sex, age, whether they wore contact lenses (hard or soft) or glasses, and whether they consumed nicotine in the 10 hours before the experiment. It also contained questions on the hours of sleep they got the night before, their handedness, whether the participants had consumed alcohol or caffeine and their level of sleepiness, but this information was not further used in this research. The second questionnaire that was used was the Morningness-Eveningness Questionnaire (MEQ) (Horne & Östberg, 1976) which contained questions about their sleeping pattern and circadian rhythm. It included 19 questions on their bedtimes and hours of sleep. This questionnaire was taken but not further used in this research.

Procedure

Participants underwent two sessions under different lighting conditions, one light session where the room in which the experiment was taken was light, and one dark condition where the room had dim lighting. Illuminance levels of the room therefore varied across conditions, with baseline in the light condition set at 7 Lux, baseline in the dark condition at 0 Lux, detection in the light condition at 3 Lux, and detection in the dark condition at 0 Lux. The order in which participants were assigned to the different conditions was counterbalanced.

A session began with participants completing an informed consent form, alongside the demographic questionnaire. In the light condition, participants also filled in the MEQ. Following this, participants underwent eye-tracker calibration. Subsequently, five minutes of baseline pupil size measurements were recorded during which participants continuously focused on the fixation dot in the middle of the screen. After this the participants underwent a second calibration of the eye-tracker. Participants then engaged in the practice task. All the actions mentioned before this were facilitated by the experimenter's presence in the room. When a participant was attending the dark session, a period of dark adaptation then ensued, during which they sat in darkness for 10 minutes before commencing the detection task. Conversely, participants proceeded directly to the detection task after completing the practice task when they were attending the light session. The experimenter was not present in the room during the dark adaptation and the detection task.

The task consisted of several trial configurations, including a practice block comprising 16 trials, of which eight where the target was visible and eight where the target was not shown. Additionally, there were three blocks of 56 trials each containing the staircase method and seven blocks of 56 trials each without the staircase method. This makes for a total task length of 576 trials. For this study only the data of the 56 trials without the staircase method were used for the analysis. To control for mind wandering, six questions related to this appeared randomly in blocks. They were presented between target 90 and target 576, this range was then cut in six equal blocks.

Data Processing and Analyses

For pre-processing of the pupil data, the module Gazepoint parser from the python package Eyelinkparser was used. Blinks were removed rather than interpolated, and the default trace processor was used. The data was cropped to one second before stimulus presentation, and the average pupil size per trial was extracted from that.

A control analysis for nicotine use was performed by looking at the correlation between nicotine use and mean pupil size in the baseline data in both lighting conditions with additional *t* tests. Afterwards a repeated measures Analysis of Covariance (ANOVA) was conducted on the detection data to look at the relation between the pupil size and detection performance across the different colors.

Results

Control Analysis for Nicotine Use

To control for the effect of nicotine use on pupil size, *t* tests and correlations were conducted between the mean pupil size in the baseline data and nicotine use in both the light and dark condition. In the light subsample eight participants used nicotine (n = 43), and in the dark subsample 11 participants used nicotine (n = 50). Neither the data in the light condition (r = 0.02, p = 0.89, t = -0.13), or in the dark condition (r = 0.02, p = 0.90, t = -0.13), showed a significant correlation with the mean pupil size, which is why participants who used nicotine were not excluded from the sample.

Detection Performance, Pupil Size and Color

Accuracy was used as a variable to measure detection performance, and pupil size was designated as either large, meaning larger than the median pupil size of the participant, or small, meaning smaller than the median pupil size.

Descriptive Statistics

The distribution of correct responses on the detection task for each color in the different conditions are presented in Figure 2, 3, 4 and 5. The mean pupil size is reported in arbitrary units. In the light subsample this was 25.9 (SD = 5.5; Min = 6.31; Max = 37.73) and in the dark subsample 25.4 (SD = 5.6; Min = 6.58; Max = 64.43).

Figure 2

Distribution of Correct/Incorrect Responses for Blue Targets in the Light Condition



Figure 3

Distribution of Correct/Incorrect Responses for Red Targets in the Light Condition



Figure 4

Distribution of Correct/Incorrect Responses for Blue Targets in the Dark Condition



Figure 5

Distribution of Correct/Incorrect Responses for Red Targets in the Dark Condition



Repeated Measures ANOVA

A repeated measures ANOVA was conducted with color as a factor with levels blue and red and pupil size as a factor with levels big and small. The Huynh-Feldt correction was performed to correct for the violated sphericity assumption in the dark condition. For an illustration of the results, see Figure 6 and 7. The effect of color (F(1, 42) = 5.36, p = .026, $\eta^2 = 0.03$) and pupil size (F(1, 42) = 23.84, p = < .001, $\eta^2 = 0.02$) on accuracy were both significant in the light condition with both a small to medium effect size. In the dark condition only the effect of pupil size on accuracy was significant with a small effect size (F(1, 49) =17.63, p = < .001, $\eta^2 = 0.01$). The effect of color did not reach statistical significance in the dark condition (F(1, 49) = 1.70, p = 0.198, $\eta^2 = 0.01$).

Contrary to our prediction that blue targets would be easier to detect in the dark condition, post hoc comparisons using the *t* test with Bonferroni correction showed that accuracy was overall higher for red targets than blue targets in both lighting conditions, but this difference was only significant in the light condition (t = -2.32, p = 0.026) with a mean difference of 0.06 (95% *CI* [0.11, -0.01]).

Figure 6

Accuracy, Pupil Size and Color in the Light Condition



Figure 7

Accuracy, Pupil Size and Color in the Dark Condition



Consistent with our expectation these post hoc comparisons showed an additional overall large pupil advantage in both the light condition (t = -4.88, p < 0.001) with a mean difference of -0.05 (95% *CI* [-0.07, -0.03]), and the dark condition (t = -4.20, p < 0.001) with a mean difference of -0.03 (95% *CI* [-0.05, -0.02]).

The interaction effect between color and pupil size was nonsignificant in both the light $(F(1, 42) = 2.19, p = 0.147, \eta^2 = 0.001)$ and the dark condition $(F(1, 49) = 1.24, p = 0.27, \eta^2 = 4.71 \times 10^{-4})$, indicating that the impact of color of the targets on detection accuracy does not significantly differ across large and small pupil sizes.

Discussion

Here we present the results of an experiment that reports different effects of psychosensory pupil size on detection performance among differently colored targets, in an attempt to better understand the way we shape perception. We measured detection performance by accuracy on a detection task with blue and red stimuli while measuring pupil size before the presentation of each target. We report that in a light environment the color of stimuli in a detection task has a significant effect on detection accuracy. We also found that the pupil size prior to the presentation of a stimulus has a significant effect on detection accuracy. Additionally, a control analysis for nicotine use showed no correlation between nicotine use and mean pupil size.

Notably, our findings confirm that large pupil size results in better detection performance, regardless of the lighting level of the environment. In our experiment larger pupil size prior to the presentation of faint stimuli resulted in a higher detection accuracy of faint stimuli. These results are consistent with the results of Mathôt & Ivanov (2019) who found a better visual sensitivity in manipulated large pupils. Our results confirm this and add to this that the effect also exists in pupil dilation caused by spontaneous pupil size changes. This better visual sensitivity is caused by the fact that more light is able to enter on the retina in dilated pupils compared to small pupils leading to a better signal-to-noise ratio (Eberhardt et al., 2021). This consistent large pupil advantage highlights the importance of considering pupil dynamics in studies of visual detection and cognitive performance.

In addition, we found an effect of color on detection performance in the light condition. Our hypothesis predicted blue targets to be better detected than red targets, based on the greater sensitivity of rod and cone cells to shorter wavelengths of light. However, the results indicated an overall higher accuracy for red targets compared to blue targets in both lighting conditions, with this difference reaching statistical significance only in the light condition. This is surprising, given the fact that rod-type cells are only able to absorb short wavelengths of light such as blue, and not red (Brown & Wald, 1964b; Reitner et al., 1991) and a higher sensitivity for blue light was also found in cone-dominated vision in mice in a recent study of Franke et al. (2022). This highlights the complexity of the underlying mechanisms and gives implications for further investigation of this color effect and the color sensitivity of rod-type and cone-type cells. One explanation for the better detection of red targets in cone-dominated vision could be that a study showed that human S-cone receptors have a lower signal-to-noise ratio than M-cones and L-cones, resulting in higher flashdetection thresholds in S-cones (Baudin et al., 2019). Since the stimuli were presented very shortly, the lower signal-to-noise ratio for L-cones could lead to higher sensitivity for red light. Another possibility is that the opacity in the staircase was adjusted too strongly for the red stimuli, making the red stimuli easier to detect than the blue stimuli. Finally, the relative amounts of rods and cones and their locations on the retina could also be explain the results found. Rods make up about 95% of the photoreceptors on the human retina and are primarily located in peripheral regions of the retina. The remaining 5%, consisting of cone photoreceptors, are located in the fovea (Curcio et al., 1990). This suggests that the eccentricity of the targets could influence whether rod- or cone-dominated vision is activated, thereby affecting the detection process. This would need to be investigated further by adding eccentricity as a variable in future studies. This effect of color was nonsignificant in the dark condition. An explanation for this could be that in darker surroundings rods are usually primarily active because they are more sensitive to light but are much less responsive to color (Ingram et al, 2016; Thoreson & Dacey, 2019).

Furthermore, this is also explained by the fact that the interaction effect between color and pupil size is nonsignificant in both conditions, suggesting that the impact of pupil size on detection accuracy is consistent across different colors of stimuli. This is not in line with the

effect found in mice in the study of Franke et al (2022), where pupil dilation alone was sufficient to switch from rod-dominated vision to cone-dominated vision. The differences between that study and the current study need further investigation. A future study could possibly examine these differences by directly measuring the activation of rods and cones., for example by using the silent substitution method (Spitschan & Woelders, 2018). This method consists of selectively stimulating different photoreceptors in the eye. This allows researchers to look at the isolated activation of rod-type cells and different cone-type cells and hereby exploring the underlying mechanisms of their function deeper. Future studies could also explore the specific conditions under which red targets gain a detection advantage and whether this is influenced by factors such as individual differences in color perception.

The control analysis on nicotine consumption did not show any relation with mean pupil size, suggesting that the participants who used nicotine did not influence the main analysis in any way. This is surprising, considering that previous studies showed pupil constriction in people who consumed nicotine prior to measurements (Lie & Domino, 1999; Wardhani et al., 2020). The fact that we did not find this effect is probably due to the small number of participants who used nicotine in our samples. Another explanation for these differences could be the amount of nicotine consumed by these participants and the timing of the measurement relative to the nicotine intake, but this would need further investigation.

Finally, a few limitations of our study are worth mentioning. First, the sample size may be considered modest. Additionally, since all participants were psychology students from a single university, the findings may not generalize to a broader population with different backgrounds or age groups. Secondly, the fixed duration of 50 milliseconds for stimulus presentation may not be optimal for detecting differences in sensitivity between blue and red targets, especially considering the inherent differences in signal-to-noise ratios for S-cones, M-cones, and L-cones (Baudin et al., 2019). Lastly, because the researchers were not present

in the room during the detection task, it is not entirely certain whether participants kept their attention on the task. Addressing these limitations in future research could improve the robustness and generalizability of the findings, providing a deeper understanding of the relationship between psychosensory pupil size, color detection, and visual perception.

To conclude, our study highlights the significant impact of psychosensory pupil size on detection performance, demonstrating that larger pupil sizes enhance the detection accuracy of faint stimuli regardless of the lighting conditions. Additionally, we found that red targets were detected more accurately than blue targets in a light environment, contrary to our hypothesis. These findings suggest a complex interaction between pupil dynamics and color sensitivity, warranting further investigation into the underlying mechanisms and conditions that influence visual processing and perception. Future research should focus on exploring the specific factors contributing to the red target advantage and the differential activation of rod and cone cells during pupil size changes.

References

Bardak, H., Gunay, M., Mumcu, U., & Bardak, Y. (2016). Effect of single administration of coffee on pupil size and ocular wavefront aberration measurements in healthy subjects. *BioMed Research International*, 2016, 1–

5. https://doi.org/10.1155/2016/9578308

- Baudin, J., Angueyra, J. M., Sinha, R., & Rieke, F. (2019). S-cone photoreceptors in the primate retina are functionally distinct from L and M cones. *eLife*, 8. https://doi.org/10.7554/elife.39166
- Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, 45(4), 602–607. <u>https://doi.org/10.1111/j.1469-8986.2008.00654.x</u>
- Brown, P. K., & Wald, G. (1964b). Visual pigments in single rods and cones of the human retina. *Science*, *144*(3614), 45–52. https://doi.org/10.1126/science.144.3614.45
- Bowmaker, J. K., & Dartnall, H. J. A. (1980). Visual pigments of rods and cones in a human retina. *The Journal of Physiology*, 298(1), 501–

511. https://doi.org/10.1113/jphysiol.1980.sp013097

- Campbell, F. W., & Gregory, A. H. (1960). Effect of size of pupil on visual acuity. *Nature*, *187*(4743), 1121–1123. <u>https://doi.org/10.1038/1871121c0</u>
- Castro, J. J., Pozo, A. M., Rubiño, M., Anera, R. G., & Del Barco, L. J. (2014). Retinal-Image Quality and Night-Vision Performance after Alcohol Consumption. *Journal of Ophthalmology*, 2014, 1–7. <u>https://doi.org/10.1155/2014/704823</u>
- Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, 292(4), 497– 523. https://doi.org/10.1002/cne.902920402

- Dacey, D. M. (1999). Primate retina: cell types, circuits and color opponency. *Progress in Retinal and Eye Research*, 18(6), 737–763. https://doi.org/10.1016/s1350-9462(98)00013-5
- Eberhardt, L. V., Strauch, C., Hartmann, T., & Huckauf, A. (2021). Increasing pupil size is associated with improved detection performance in the periphery. *Attention, Perception, & Psychophysics*, 84(1), 138–149. <u>https://doi.org/10.3758/s13414-021-02388-w</u>
- Ebitz, R. B., & Moore, T. (2019). Both a gauge and a filter: cognitive modulations of pupil size. *Frontiers in Neurology*, 9. <u>https://doi.org/10.3389/fneur.2018.01190</u>
- Ebrey, T., & Koutalos, Y. (2001). Vertebrate photoreceptors. *Progress in Retinal and Eye Research*, 20(1), 49–94. https://doi.org/10.1016/s1350-9462(00)00014-8
- Eckstein, M. K., Guerra-Carrillo, B., Singley, A. T. M., & Bunge, S. A. (2017). Beyond eye gaze: What else can eyetracking reveal about cognition and cognitive development? *Developmental Cognitive Neuroscience*, 25, 69–

91. https://doi.org/10.1016/j.dcn.2016.11.001

- Ellis, C. J. (1981). The pupillary light reflex in normal subjects. *British Journal of Ophthalmology*, 65(11), 754–759. https://doi.org/10.1136/bjo.65.11.754
- Fietz, J., Pöhlchen, D., Binder, F. P., Czisch, M., Sämann, P. G., & Spoormaker, V. I. (2021).
 Pupillometry tracks cognitive load and salience network activity in a working memory functional magnetic resonance imaging task. *Human Brain Mapping*, *43*(2), 665–680. https://doi.org/10.1002/hbm.25678
- Franke, K., Willeke, K. F., Ponder, K., Galdamez, M., Zhou, N., Muhammad, T., Patel, S. S., Froudarakis, E., Reimer, J., Sinz, F. H., & Tolias, A. S. (2022). State-dependent pupil dilation rapidly shifts visual feature selectivity. *Nature*, *610*(7930), 128– 134. https://doi.org/10.1038/s41586-022-05270-3

- Granholm, E., & Steinhauer, S. R. (2004). Pupillometric measures of cognitive and emotional processes. *International Journal of Psychophysiology*, 52(1), 1–
 <u>https://doi.org/10.1016/j.ijpsycho.2003.12.001</u>
- Horne, J., & Östberg, O. (1976). A self-assessment questionnaire to determine morningnesseveningness in human circadian rhythms. *Int J Chronobiol*, 4(2), 97– 110. <u>https://ci.nii.ac.jp/naid/20001543451</u>
- Ingram, N. T., Sampath, A. P., & Fain, G. L. (2016). Why are rods more sensitive than cones? *Journal of Physiology*, *594*(19), 5415–5426. https://doi.org/10.1113/jp272556
- Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between Pupil Diameter and Neuronal Activity in the Locus Coeruleus, Colliculi, and Cingulate Cortex. *Neuron*, 89(1), 221–234. https://doi.org/10.1016/j.neuron.2015.11.028
- Kankipati, L., Girkin, C. A., & Gamlin, P. D. (2010). Post-illumination Pupil Response in Subjects without Ocular Disease. *Investigative Ophthalmology & Visual Science*, 51(5), 2764. <u>https://doi.org/10.1167/iovs.09-4717</u>
- Levin, E. D., Conners, C. K., Silva, D., Hinton, S. C., Meck, W. H., March, J. S., & Rose, J. E. (1998). Transdermal nicotine effects on attention. *Psychopharmacology/Psychopharmacologia*, 140(2), 135–141. https://doi.org/10.1007/s002130050750
- Lie, T. C., & Domino, E. F. (1999). Effects of tobacco smoking on the human pupil. *PubMed*, *37*(4), 184–188. <u>https://pubmed.ncbi.nlm.nih.gov/10235421</u>
- Mathôt, S., & Ivanov, Y. (2019). The effect of pupil size and peripheral brightness on detection and discrimination performance. *PeerJ*, *7*, e8220. https://doi.org/10.7717/peerj.8220

- Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, 44(2), 314–324. https://doi.org/10.3758/s13428-011-0168-7
- Mathôt, S., & Vilotijević, A. (2022). Methods in cognitive pupillometry: Design,
 preprocessing, and statistical analysis. *Behavior Research Methods*, 55(6), 3055–3077. <u>https://doi.org/10.3758/s13428-022-01957-7</u>
- Mullen, K. T., Sakurai, M., & Chu, W. P. (2005). Does L/M cone opponency disappear in human periphery? *Perception*, 34(8), 951–959. <u>https://doi.org/10.1068/p5374</u>
- Murphy, P. R., Robertson, I. H., Balsters, J. H., & O'connell, R. G. (2011). Pupillometry and P3 index the locus coeruleus–noradrenergic arousal function in humans. *Psychophysiology*, 48(11), 1532–1543. https://doi.org/10.1111/j.1469-8986.2011.01226.x
- Reitner, A., Sharpe, L. T., & Zrenner, E. (1991). Is colour vision possible with only rods and blue-sensitive cones? *Nature*, *352*(6338), 798–800. https://doi.org/10.1038/352798a0
- Schneider, M., Hathway, P., Leuchs, L., Sämann, P. G., Czisch, M., & Spoormaker, V. I.
 (2016). Spontaneous pupil dilations during the resting state are associated with activation of the salience network. *NeuroImage*, *139*, 189–

201. https://doi.org/10.1016/j.neuroimage.2016.06.011

- Spitschan, M., & Woelders, T. (2018). The method of silent substitution for examining melanopsin contributions to pupil control. *Frontiers in Neurology*, 9. https://doi.org/10.3389/fneur.2018.00941
- Stolte, M., Gollan, B., & Ansorge, U. (2020). Tracking visual search demands and memory load through pupil dilation. *Journal of Vision*, 20(6), 21. <u>https://doi.org/10.1167/jov.20.6.21</u>

- Sulutvedt, U., Zavagno, D., Lubell, J., Leknes, S., De Rodez Benavent, S. A., & Laeng, B.
 (2021). Brightness perception changes related to pupil size. *Vision Research*, *178*, 41–47. https://doi.org/10.1016/j.visres.2020.09.004
- Thoreson, W. B., & Dacey, D. M. (2019). Diverse cell types, circuits, and mechanisms for color vision in the vertebrate retina. *Physiological Reviews*, 99(3), 1527– 1573. <u>https://doi.org/10.1152/physrev.00027.2018</u>
- Van Egroo, M., Gaggioni, G., Cespedes-Ortiz, C., Ly, J. Q. M., & Vandewalle, G. (2019).
 Steady-State Pupil Size Varies with Circadian Phase and Sleep Homeostasis in
 Healthy Young Men. *Clocks & Sleep*, 1(2), 240–
 258. https://doi.org/10.3390/clockssleep1020021
- Wardhani, I. K., Mathôt, S., Boehler, C. N., & Laeng, B. (2020). Effects of nicotine on pupil size and performance during multiple-object tracking in non-nicotine users. *International Journal of Psychophysiology*, *158*, 45–55. https://doi.org/10.1016/j.ijpsycho.2020.09.005
- Wilhelm, B., Stuiber, G., Lüdtke, H., & Wilhelm, H. (2013). The effect of caffeine on spontaneous pupillary oscillations. *Ophthalmic and Physiological Optics/Ophthalmic & Physiological Optics*, 34(1), 73–81. https://doi.org/10.1111/opo.12094
- Wilhelm, B., Wilhelm, H., Lüdtke, H., Streicher, P., & Adler, M. (1998). Pupillographic assessment of sleepiness in sleep-deprived healthy subjects. *Sleep*. https://doi.org/10.1093/sleep/21.3.258
- Yoshioka, T., Dow, B. M., & Vautin, R. G. (1996). Neuronal mechanisms of color categorization in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research*, 76(1–2), 51–70. https://doi.org/10.1016/0166-4328(95)00183-2

Appendix

I hereby declare that parts of the grammar and spelling in this thesis were reviewed with the assistance of ChatGPT, an AI language model developed by OpenAI. This tool was utilized to check and enhance the accuracy of the written content.