The effect of covert visual attention on pupil size during perceptual fading

Ana Vilotijević[1,*] and Sebastiaan Mathôt[1]

[1]Department of Psychology, University of Groningen, 9712TS Groningen, The Netherlands

*Address for correspondence: a.vilotijevic@rug.nl

Abstract

Pupil size is modulated by various cognitive factors such as attention, working memory, mental imagery, and subjective perception. Previous studies examining cognitive effects on pupil size mainly focused on inducing or enhancing a subjective experience of brightness or darkness (for example by asking participants to attend to/ memorize a bright or dark stimulus), and then showing that this affects pupil size. Surprisingly, the inverse has never been done; that is, it is still unknown what happens when a subjective experience of brightness or darkness is eliminated or strongly reduced even though bright or dark stimuli are physically present. Here, we aim to answer this question by using perceptual fading, a phenomenon where a visual stimulus gradually fades from visual awareness despite its continuous presentation. The study contains two blocks: Fading and Non-Fading. In the Fading block, participants were presented with black and white patches with a fuzzy outline that were presented at the same location throughout the block, thus inducing strong perceptual fading. In contrast, in the Non-Fading block, the patches switched sides on each trial, thus preventing perceptual fading. Participants covertly attended to one of the two patches, indicated by a cue, and reported the offset of one of a set of circles that are displayed on top. We hypothesized that pupil size will be modulated by covert visual attention in the Non-Fading block, but that this effect will not (or to a lesser extent) arise in the Fading block. We found that covert visual attention to bright/ dark does modulate pupil size even during perceptual fading (Fading block), but to a lesser extent than when the perceptual experience of brightness/ darkness is preserved (Non-Fading block). This implies that pupil size is always modulated by covert attention, but that the effect decreases as subjective experience of brightness or darkness decreases. In broader terms, this suggests that cognitive modulations of pupil size reflect a mixture of high-level and lower-level visual processing.

Keywords: pupil size, covert attention, adaptation, perceptual fading

Introduction

Pupil size is modulated by cognitive factors such as attention, working memory, mental imagery, and subjective perception (*attention*: e.g., Binda et al., 2014; Binda & Murray, 2015; Bombeke et al., 2016; Mathôt et al., 2013; Naber & Nakayama, 2013; Unsworth & Robison, 2017; Vilotijević & Mathôt, 2023a, 2023b; *working memory*: e.g., Hustá et al., 2019; Keene et al., 2022; Koevoet et al., 2023; Wilschut & Mathôt, 2022*; mental imagery*: e.g., Laeng & Sulutvedt, 2014; *subjective perception*: e.g., Binda et al., 2013; for reviews see Koevoet et al., 2023; Mathôt, 2020; Vilotijević & Mathot, 2023c). However, even though the conditions under which pupil size is modulated by cognition have been well characterized, much is still unclear about the physiological mechanisms through which this happens.

Previous studies have consistently shown that pupil size is modulated by covert visual attention (Binda et al., 2014; Mathôt et al., 2013; Naber et al., 2013; Unsworth & Robison, 2017). For instance, Mathôt et al. (2013) conducted a study in which participants were presented with a display that was vertically divided into bright and dark halves. Participants were cued towards either the bright or the dark side by an informative cue that predicted the location of an upcoming target. Results showed modulation of pupil size by covert visual attention: when participants covertly focused on the bright side, the pupil constricted more as compared to when participants covertly focused on the dark side, despite constant visual input and gaze fixation.

Similarly, Binda and colleagues (2013) showed that subjective perception modulates pupil size. In their study, participants were presented with naturalistic images of the sun and the moon that were carefully matched in luminance. The participants' task was to classify whether these images represented the sun or the moon. Results showed modulation of pupil size by subjective interpretation: when participants identified an image as the sun, their pupils constricted more as compared to when they identified an image as the moon, despite the images being matched in luminance.

Although studies such as those reviewed above have clearly shown that pupil size is modulated by cognitive factors, very little is known about the underlying physiological and cognitive mechanisms. Therefore, we recently conducted a study to better understand the underlying mechanisms (Vilotijević & Mathôt, 2023a); specifically, we focused on the question of whether modulation of pupil size by covert visual attention is mediated only by the so-called image-forming pathway, which is associated with rods and cones (Schmidt & Kofuji, 2008), or whether this is also mediated by the non-image-forming pathway, which is associated with intrinsically photosensitive retinal ganglion cells (ipRGCs) (non-human studies: Berson, 2003; human studies: Zele et al., 2011; Provencio et al., 2000; Barrionuevo et al., 2023; reviews: Schmidt & Kofuji, 2008; McDougal & Gamlin, 2015). To test this, we manipulated the color (blue/ red) of a to-be-attended stimulus in a spatial cueing paradigm, leveraging the fact that ipRGCs are predominantly responsive to blue light and thus cause the most prominent sustained constriction in response to blue light. Participants covertly attended to either dim or bright stimuli that were either red or blue for a prolonged period (15s). We replicated the classic effect of covert visual attention on pupil size as discussed above, finding that the pupil constricted more when covertly attending to bright as compared to dim stimuli (with the same color). However, we did not find any difference in pupil size when covertly attending to blue as compared to red stimuli (with the same luminosity), whereas we did observe this difference when participants directly looked at the same blue or red stimuli (a classic marker of the influence of ipRGCs on pupil size). This implies that the effect of covert visual attention (and perhaps cognitive factors more generally) on pupil size is mainly mediated by the image-forming rod-and-cone pathway, and not by the non-image-forming ipRGC pathway. This finding goes some way towards understanding the physiological and cognitive mechanisms behind the influence of cognitive factors on pupil size.

However, the image-forming pathway itself is complex and hierarchical and it is still unclear which level of processing is reflected in cognitive effects on pupil size. To date, studies have mainly focused on inducing a subjective experience of brightness or darkness, and showing that this affects pupil size (Binda et al., 2014; Binda & Murray, 2015; Bombeke et al., 2016; Mathôt et al., 2013; Naber & Nakayama, 2013; Unsworth & Robison, 2017; Vilotijević & Mathôt, 2023). Surprisingly, the inverse has never been done; that is, it is still unknown what happens when a subjective experience of brightness or darkness is eliminated or strongly reduced even though bright or dark stimuli are physically present. Do cognitive modulations of pupil size disappear along with the subjective experience of brightness or darkness? This is the question that we aim to test in the present study.

To do so, we made use of perceptual fading, a phenomenon where a fuzzy visual stimulus gradually disappears from perception or becomes less noticeable, despite the visual stimulus remaining physically present (Clarke, 1961; Kanai & Kamitani, 2003; Troxler, 1804). Perceptual fading is commonly explained through adaptation, but it is a distinct phenomenon (Bachy & Zaidi, 2014). Adaptation, in the sense that we use the term here, refers to the fact that photoreceptors and other neurons involved in the early stages of visual processing quickly reduce their firing rate after prolonged exposure to a stimulus (Fain et al., 2001; Kohn, 2007; Laughlin, 1989; McDougal & Gamlin, 2010; Stockman & Brainard, 2010; Webster, 2015). The extent and precise time course of adaptation depends on many factors, but it is in general a fast process that occurs within seconds (Kohn, 2007; Webster, 2015). However, adaptation does not always translate to a change in perception, because the visual system relies on many cues to keep perception stable despite changes in sensory input, including adaptation state. As a case in point, a bright circle with sharp edges is not susceptible to perceptual fading, presumably because the edges move in out of the receptive fields of photoreceptors, thus preventing adaptation of the edge, which serves as a cue that the circle is “still there” and in turn prevents perceptual fading of the circle as a whole: the visual system does not need much to understand that stimuli do not simply disappear. And even a bright circle with fuzzy edges fades from perception much more slowly than you would expect based on the time course of adaptation, presumably because the visual system relies on a heuristic of stability that keeps the perception of the circle intact for some time. Conversely, complete perceptual fading also does not require complete adaptation (Hsieh & Colas, 2012). Again as a case in point, a fuzzy bright circle fades—given enough time—from perception almost entirely, even though under conditions of normal display viewing, photoreceptors never become entirely silent (Krauskopf, 1963; Ramachandran et al., 1993). Taken together, and admitting that the exact relationship between adaptation and perceptual fading is not fully understood, perceptual fading appears to be a high-level phenomenon that is related to low-level adaption but is not identical to it, and that reflects visual awareness (Clarke & Belcher, 1962; Hsieh & Colas, 2012; Kanai & Kamitani, 2003; Kotulak & Schor, 1986; Ramachandran et al., 1993; Sheth & Shimojo, 2004). As such, it is an important question whether attending to a bright versus a dark stimulus affects pupil size, even when due to perceptual fading the stimulus is no longer perceived.

In the present study, we induced near-complete perceptual fading and thus diminished the subjective experience of brightness while still keeping the stimuli physically present on the screen. To this end, the study comprised two blocks: Fading and Non-Fading. In the Fading block, participants were exposed to a visual display containing fuzzy black and white patches that are continuously shown on the same side of a gray screen. Both patches were overlaid with randomly dispersed circles. Participants received a cue pointing to either the left or the right, and their task was to covertly attend to the indicated side and detect the offset of a single circle. In the Non-Fading block, the task was the same, except that the white and black patches switched sides on each trial, thus preventing perceptual fading.

Finally, our main hypothesis was that pupil size will be modulated by covert visual attention to bright/ dark in the Non-Fading block, but not (or to a lesser extent) in the Fading block. This would imply that cognitive modulations of pupil size (gradually) disappear along with the subjective experience of brightness or darkness, which would in turn suggest that cognitive

modulations of pupil size depend at least in part on a high level of visual processing.

Hypotheses

We tested the following hypotheses (see Table 1):

Hypothesis 1: Covert visual attention to bright/ dark modulates pupil size in the Non-Fading block. We predicted the pupil size to be modulated by the brightness of covertly attended stimuli in the Non-Fading block. Specifically, we predicted to observe smaller pupils when covertly attending to the bright stimulus compared to the dark stimulus in the Non-Fading block. This served as a sanity check in our study given that this finding is already well-established (Binda et al., 2014; Binda & Murray, 2015; Bombeke et al., 2016; Mathôt et al., 2013; Vilotijević & Mathôt, 2023).

Hypothesis 2: Pupil size is smaller in the Non-Fading as compared to the Fading block. We predicted a pattern of the typical pupil response to visual change in the Non-Fading block, as a result of the switches that occur from trial to trial (Ellis, 1981; Hong et al., 2001; Mathôt, 2018). We predicted this response to include a rapid constriction immediately after the display onset, followed by a subsequent pupil escape, and eventually a response modulated by covert attention following the cue onset. We predicted that this pattern will lead to smaller pupil sizes during the Non-Fading block compared to the Fading block. This was not a hypothesis of interest, but also served as a sanity check because it is a strong prediction based on the general properties of the pupil response to visual change.

Hypothesis 3.1: Covert visual attention to bright/ dark does not modulate pupil size in the Fading block during full perceptual fading. This hypothesis holds that pupil size is *not* modulated by the brightness of covertly attended stimuli in the Fading block in the subset of trials where participants report maximal perceptual fading (adaptation self-report levels: 2 and 3). Specifically, this hypothesis predicted no differences in pupil responses when covertly attending to the bright stimulus and the dark stimulus in the Fading block. If confirmed, this finding would imply that pupil size is not modulated by covert attention once the subjective experience of brightness or darkness has disappeared. In broader terms, this would suggest that cognitive modulations of pupil size solely reflect a high level of visual processing.

Hypothesis 3.2: Covert visual attention to bright/ dark does modulate pupil size in the Fading block during full perceptual fading, but the effect is smaller than in the Non-Fading block. This hypothesis holds that pupil size is modulated by the brightness of covertly attended stimuli also in the Fading block in the subset of trials where participants report maximal perceptual fading (adaptation self-report levels: 2 and 3), but that the effect will be reduced as compared to the effect in the Non-Fading block. If confirmed, this finding would imply that pupil size is always modulated by covert attention, but that the effect decreases as subjective experience of brightness or darkness decreases. In broader terms, this would suggest that cognitive modulations of pupil size reflect a mixture of high-level and lower-level visual processing.

Hypothesis 4: The effect of covert visual attention on pupil size decreases over time in the Fading block but not in the Non-Fading block. We predicted that the strength of perceptual fading will increase over the course of the Fading block, in turn resulting in decreased modulation of pupil size by covert attention. If confirmed, this finding would imply that the effect of covert attention gradually decreases along with the gradually decreasing experience of brightness/ darkness. In contrast, we predicted that the modulation of pupil size by covert attention will remain the same over the course of the Non-Fading block, because there the experience of brightness/ darkness will stay intact.

Hypothesis 5: The effect of covert visual attention on pupil size decreases with increasing self-reported perceptual fading in the Fading block. We predicted an interaction between Fading Self-Report and Covertly Attended Brightness on Pupil Size in the Fading block, reflecting that the effect of covert attention on pupil size is inversely related to the subjective level of perceptual fading.

Hypothesis 6: The accuracy of responses is higher in validly cued trials compared to invalidly cued trials. We predicted a main effect of Cue Validity on Accuracy in both Fading and Non-Fading blocks. This served as an attention check in our study given that the cueing effect is well-established and would serve as a confirmation of Posner’s theory of spatial attention (Posner, 1980) and attentional deployment in our study.

Table 1. Study design template

Research question	
Do cognitive modulations of the PLR disappear along with the subjective experience of brightness or darkness?	
The design	
Experimental design	Within-subjects design
Dependent variables	Pupil size
Independent variables (with respective levels)	Covertly attended brightness (bright vs. dark); Block type (Fading vs. Non-Fading); Trial number
Non-independent predicting variables (with respective levels)	Fading Self-Report (0,1,2,3)
Counterbalancing	- Block order will be counterbalanced across participants. - The side of bright/ dark patches in the Fading block will be counterbalanced across participants.
Hypotheses, analyses plan and prospective interpretation	

Research question	**Hypothesis**	**Sampling plan**	**Analysis plan**	**Rationale for deciding the sensitivity of the test for confirming or disconfirming the hypothesis**	**Interpretation given different outcomes**	**Theory that could be shown wrong by the outcomes**
	🟩 Quality check hypotheses					
	Neutral hypotheses					

	Of interest hypotheses					
Does covert visual attention to bright/ dark affect pupil size?	**Hypothesis 1:** Covert visual attention to bright/ dark modulates the PLR in the Non-Fading block.	We estimated sample size using the `simR` package (Green & MacLeod, 2016). Specifically, we used pilot data (*N* = 2) and selected all the trials from the Non-fading block and trials from the Fading block where participants reported high levels of adaptation (ratings of 2 and 3) to test the interaction effect between Covertly attended brightness and Block type on Pupil size (Hypothesis 3). The model included Mean pupil size as a dependent variable, Covertly attended brightness, Block type, and their	We will include only the trials from the Non-Fading block. The model will include Pupil size as dependent variable, Covertly attended brightness as fixed effect, and Participant as random effect.	For all analyses below, we will run a cross-validation in combination with linear mixed effects (LME) to localize and test effects using the Python library time_series_test. This is a preferred approach in analyzing pupillary data that we explain in detail in Mathôt & Vilotijević (2022). We will use four-fold cross-validation, such that 75% of the data will be used as a training set and the remaining 25% as a test set. As the dependent measure we will use pupil size during the	Hypothesis 1 will be confirmed by an effect of Covertly attended brightness on Pupil size on the Non-Fading block trials in the predicted direction. This finding serves as a sanity check in our study and would replicate previous studies on the effect of covert attention on pupil size.	
Does covert visual attention to bright/ dark affect pupil size differently when the subjective experience of brightness or darkness is eliminated (during	**Hypothesis 2:** Pupil size is smaller in the Non-Fading as compared to the Fading block.		We will include all trials from both blocks. The model will include Pupil size as the dependent variable, Block type as fixed effect, and		Hypothesis 2 will be confirmed by an effect of Block Type on Pupil size in the predicted direction. This finding serves also as a sanity	

perceptual fading) and when it is maintained?		interaction as fixed effects, and random effects for participants. The power analysis revealed that a sample of 30 participants would be required in order for the interaction effect to be detected with a power of 100% and an alpha level of .02. Therefore, our target sample size will be 30 participants (psychology students at the University of Groningen) for the experiment.	Participant as random effect.	covertly attended period, that is, from cue onset until 4 s later. We will use a maximal random-effects structure, which means that we include by-participant random intercepts and slopes for all fixed effects and interactions. We will use an alpha level of .02. For hypotheses that predict a null result (3.1 and 4), we will also perform a Bayesian linear mixed effects model; this model will have the same fixed- and random-effects structure as the regular model, and use the same dependent variable (i.e. as determined by	check because it is a strong prediction based on the general properties of the pupil response to visual change.	
Does covert visual attention to bright/ dark affect pupil size during perceptual fading?	**Hypothesis 3.1.:** Covert visual attention to bright/ dark does not modulate pupil size in the Fading block during full perceptual fading.		We will use all trials from the Non-Fading block and trials from the Fading block where participants reported high levels of adaptation (ratings of 2 and 3), to ensure full perceptual fading. The model will include Pupil size as the dependent variable, Covertly attended brightness, Block type (with Fading block as reference), and their interaction as fixed effects, and Participant as random effect.		Hypothesis 3.1 and 3.2 will both be confirmed by an interaction between Block Type and Covertly attended brightness in the predicted direction. Hypothesis 3.1 will be confirmed by the absence of a main effect of Covertly attended brightness (which will relate to the Fading block because it is the reference) in the predicted direction, and evidence for the null hypothesis for this effect as indicated by the corresponding Bayesian linear	Theoretically, the notion that modulations of pupil size by covert visual attention reflect a high level of visual processing could be (un)supported by our proposed analysis. If neither of 3.1. Or 3.2. Hypothesis comes out, the idea that modulations of pupil size by covert visual attention reflect high levels of visual processing will be refuted.
	Hypothesis 3.2.: Covert visual attention to bright/ dark does modulate pupil size in the Fading block during full perceptual fading, but the effect is smaller than in the Non-Fading block.					

				cross-validation); we will use the default parameters for Bayesian linear mixed models as implemented in JASP. These hypotheses will be confirmed if the BF in favor of the null hypothesis for the predicted effect exceeds 3.	mixed model (both are required). Hypothesis 3.2 will be confirmed by the presence of a main effect of Covertly attended brightness. Confirming Hypothesis 3.1. would imply that PLR is not modulated by covert attention once the subjective experience of brightness or darkness is lacking. In broader terms, this would suggest that cognitive modulations of the PLR are dependent on subjective perception and rely solely on a high level of visual processing. However, confirming Hypothesis 3.2 would imply that	

					PLR is modulated by covert attention, but the effect decreases as the subjective experience of brightness or darkness decreases. In broader terms, this would suggest that cognitive modulations of the PLR reflect a mixture of high-level and lower-level visual processing.	
Does the effect of covert visual attention to bright/ dark on pupil size differ over time during perceptual fading?	**Hypothesis 4:** The effect of covert visual attention on the pupil size decreases over time in the Fading block but not in the Non-Fading block.		We will include all trials. The model will include Pupil size as the dependent variable, Block type (with Fading as reference), Covertly attended brightness, Trial number, and their interactions as fixed effects, and Participant as		Hypothesis 4 will be confirmed by the absence of a two-way interaction between Covertly attended brightness and Trial number for Non-Fading blocks (which we will test using a post-hoc contrast, because Non-Fading is not	

			random effect. Hypothesis 4 will be confirmed by the presence of a three-way interaction between Covertly attended brightness, Trial number, and Block type on Pupil size in the predicted direction.		the reference), and evidence for the null hypothesis for this effect as indicated by the corresponding Bayesian linear mixed model (both are required). This finding would imply that the effect of perceptual fading strengthened over the Fading block course and that covert attention effect decreases as participants' vision gets more adapted.	
Does the effect of covert visual attention to bright/ dark on pupil size during perceptual fading depend on a self-reported level of perceptual fading?	**Hypothesis 5:** The effect of covert visual attention on pupil size decreases with increasing self-reported perceptual fading in the Fading block.		We will include the trials from the Fading block. The model will include Pupil size as the dependent variable, Covertly attended brightness, Fading self-report, and their interaction as fixed effects, and		Hypothesis 5 will be confirmed by the presence of an interaction between Covertly attended brightness and Fading self-report in the predicted direction.	

			Participant as random effect.		This finding would imply that the effect of covert attention decreases as participants’ vision gets more adapted. In broader terms, this would suggest that cognitive modulations of the PLR are dependent on subjective perception and rely on a high level of visual processing.	
Does the cue validity have an effect on accuracy?	**Hypothesis 6:** The accuracy of responses is higher in validly cued trials compared to invalidly cued trials.		We will include all trials. To test the behavioral cueing effect, we will run Generalized Linear Mixed Models (GLMM) to test a model that includes Accuracy as dependent variable, Cue validity and Block type as the fixed effects, and and Participant as random effect.		Hypothesis 6 will be confirmed by the presence of a main effect of Cue validity on Accuracy in the predicted direction.	Posner’s theory of spatial attention would be confirmed.

Quality-check measures
Participants for whom the staircase procedure did not converge will be excluded and replaced. Since it is very difficult to predict staircase behavior, convergence will be determined post-hoc and transparently reported.

Methods

The data and the analysis script are available here.

The experiment is available here.

The Stage 1 registration is available here.

Participants

In order to estimate a target sample size we conducted a power analysis using the `simR` package (Green & MacLeod, 2016). Specifically, we used pilot data (*N* = 2), collected on a version of the experiment that is very similar though not identical to the one that we tested here, and selected all the trials from the Non-fading block and trials from the Fading block where participants reported high levels of adaptation (ratings of 2 and 3) to test the interaction effect between Covertly attended brightness and Block type on Pupil size (Hypothesis 3). The model included Mean pupil size as a dependent variable, Covertly attended brightness, Block type, and their interaction as fixed effects, and random effects for participants. The power analysis revealed that a sample of 30 participants would be required in order for the interaction effect to be detected with a power of 100% and an alpha level of .02.

Therefore, 30 participants were recruited and participated in the experiment. All participants had normal or corrected-to-normal vision. Participants provided informed consent before the start of the experiment. Participants received course credits for their participation. On the basis of a checklist developed by the Ethical committee (EC-BSS) at the University of Groningen, the study was exempt from full ethical review (PSY-2324-S-0103).

Apparatus and stimuli

The experiment was programmed in OpenSesame (Mathôt et al., 2012) using PyGaze for eye tracking (Dalmaijer et al., 2014). Stimuli were presented on a 27-inch PROLITE G2773HBS-GB1 (EOL) monitor (1,920 × 1,080 pixels resolution; refresh rate: 60 Hz; maximum output: 300 cd/m^2 typical; gamma-calibrated) and an Eyelink 1000 (sampling frequency of 1000 Hz; SR Research Ltd., Mississauga, Ontario, Canada), was used for eye tracking. The experiment was conducted in a dimly lit room (lab illuminance: 39 lux).

Procedure

Prior to the start of the experiment, after making sure that the participant is well seated at about 60 cm away from the computer, an eye-tracking calibration-validation procedure was run. A chin-rest was used to keep the participant's head in a stable position. In addition to the calibration-validation procedure, a 1-point eye-tracker recalibration (“drift-correction”) was performed before each trial.

Participants were exposed to a display that features white ($SD_{grating}$: 5.77°; 99.60 cd/m2) and black ($SD_{grating}$: 5.77°; 0.14 cd/m^2) patches, one on each side (the eccentricity of the patches center from the fixation dot: 14.14°), superimposed on a gray background (23.94 cd/m^2). On top of both patches, 10 randomly dispersed unfilled circles ($r = 0.15°$) with maroon outline were presented. Each trial began with a presentation of a gray fixation dot at the center of the display for .5s, that was followed by a cue presentation lasting for 1s. The cue was a gray arrow, pointing either left or right, and indicating the side to which participants should covertly attend. Next, on 50% of trials, one randomly chosen circle (the target) disappeared. The target disappeared from the cued side in 80% of cases, and its offset occurred at a random moment in between 3 and 5s.

Participants’ task was to keep fixating at the center of the screen throughout the experiment and only covertly attend to the cued side, detect the offset of the target, and report it by pressing a ‘space’ key as fast as possible and to withhold a response on no-target-offset trials. Finally, participants were prompted to report the extent of fading they experienced at the moment that the question appeared (i.e. a retrospective judgment at the end of the trial). They reported this by using arrow keys corresponding to a four-point Likert scale (left (0) = *not at all*; down (1) = *just a bit*; up (2) = *almost fully*; right (3) = *completely*).

The experiment consisted of two blocks: Fading and Non-Fading. The Fading block contained trials where white and black patches are always presented on either the left or right side respectively (counterbalanced across participants). This meant that the display was constant throughout the block, and the only thing that changed from trial to trial were the circles that were superimposed on the patches. On the other hand, the Non-Fading block contained trials where white and black patches switched sides from trial to trial (e.g. the white patch was on the left on one trial, but on the right on the next trial).

To ensure that the accuracy is maintained at approximately 75% across all conditions, we implemented a Single-Interval Adjustment-Matrix (SIAM) procedure (Kaernbach, 1990). We staircased the opacity of the circles based on the participant’s response: after a hit, the opacity of the offsetting circle was decreased for 1% (thus increasing task difficulty); after a miss, the opacity of the offsetting circle was increased for 3% (thus decreasing task difficulty); after a false alarm, the opacity of the offsetting circle was increased for 4% (thus increasing task difficulty); after a correct rejection, no adjustments were made (thus not changing task difficulty).

The order of blocks was counterbalanced across participants. Before each block, participants completed a practice round (20 trials). Each block consisted of 120 experimental trials.

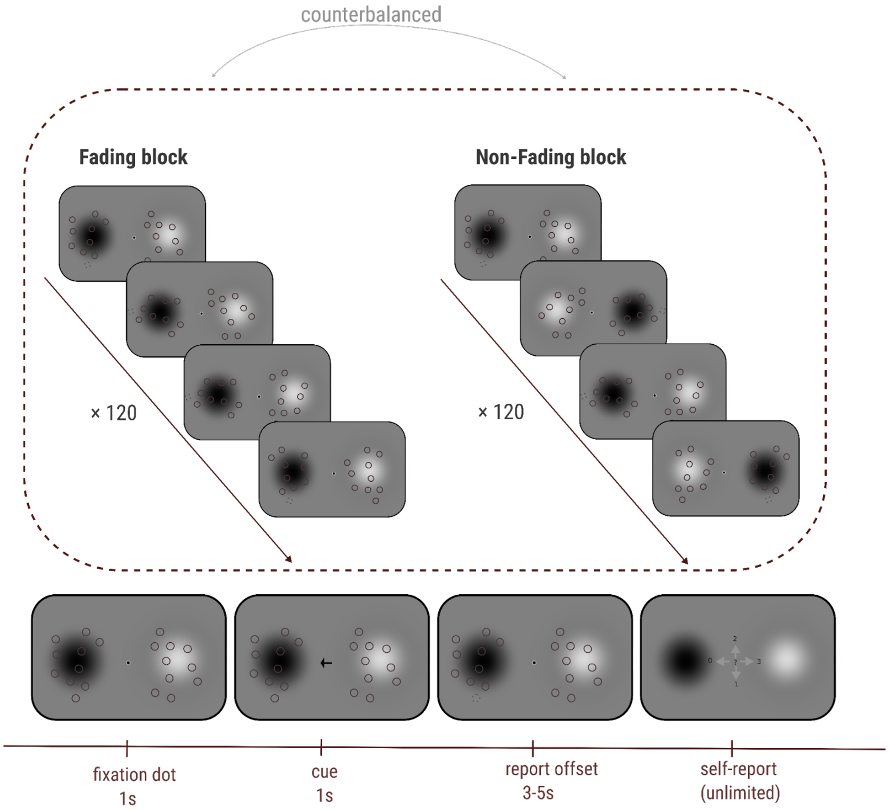

Figure 1. An example of a trial sequence in the experiment for both Fading and Non-Fading blocks. Participants were exposed to a display that features white and black patches, one on each side, superimposed on a gray background. On top of the patches, 10 randomly dispersed unfilled circles were presented on both sides. Each trial began with a presentation of a fixation dot for 1s, that is followed by a cue lasting for 1s, indicating the side to which participants should covertly attend. Next, on 50% of trials, one randomly chosen circle (the target) disappeared. Participants' task was to covertly attend to the cued side, detect the offset of the target, and report it (or withhold a response on no-target-offset trials). Finally, participants were prompted to report the extent of fading they experienced using a four-point Likert scale (left (0) = *not at all*; down (1) = *just a bit*; up (2) = *almost fully*; right (3) = *completely*). The Fading block consisted of trials where white and black patches were always presented to either left or right side respectively. On the other hand, the Non-Fading block consisted of trials where white and black patches switched sides from trial to trial.

~~**Results**~~*Data exclusion*

First, we checked whether participants made eye movements and excluded trials in which the deviation from the center of the screen was larger than 3° (distance from the fixation point toward the inner edge of the patches) for more than 100 ms consecutively (1269 trials excluded). Trials containing baseline pupil sizes of ±2 z-scores were considered outliers, and hence excluded from the data (393 trials excluded). In total, 1662 trials (23.08%) were excluded from the data.

Data preprocessing

As regards the analysis of the experimental data, we preprocessed pupillary data as follows (Mathôt & Vilotijević, 2022): we epoched the pupil data, that is, segmented it into the time window of interest. For all hypotheses except Hypothesis 2, the epoch of interest started at the cue display onset and ended just before the target's offset; this resulted in epochs of maximum 6s and minimum of 4s. As regards Hypothesis 2, we included the fixation period into the epoch of interest as testing this hypothesis relies on the activity during the fixation period. Next, segments of data that contain eye blinks were reconstructed using the `blinkreconstruct()` function from Python `DataMatrix.` (Deviation from preregistration: we preregistered that the fixation period would be included in the data for all Hypotheses. However, the fixation period induces a pupil constriction that differs slightly between conditions as a result of the interleaved staircase procedure, which changes the visual stimuli during fixation. We therefore chose to exclude the fixation period in order to avoid this differential pupil constriction from potentially confounding the main results.) All pupil data was down-sampled from 1000 to 100 Hz, and converted to millimeters of diameter according to our lab-specific formula (Wilschut & Mathôt, 2022). Also, we applied baseline correction (for details see General statistical approach).[1]

Data ~~exclusion¶~~

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~~Data~~ analyses

General statistical approach. For all analyses below, we ran a cross-validation in combination with linear mixed effects (LME) to localize and test effects using the Python library `time_series_test`. This is a preferred approach in analyzing pupillary data that we explain in detail in Mathôt & Vilotijević (2022). We used four-fold cross-validation, such that 75% of the data will be used as a training set and the remaining 25% as a test set. For testing all hypotheses except Hypothesis 2, we used pupil size during the covertly attended period, that is, from cue onset until the earliest target's offset as the dependent measure. Here, the pupil trace was baseline corrected relative to 50ms after the cue onset. Importantly, in order to test Hypothesis 2, which relies on the activity during the fixation period, we used pupil size from the fixation onset until

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[1] We did not explicitly mention this step in the Stage 1 of the Registered Report; however, baseline correction is a standard and necessary procedure for comparing effects across conditions. This ensures the reliability and validity of our findings. For a detailed explanation of this method, please refer to our methodological paper (Mathôt & Vilotijević, 2022).

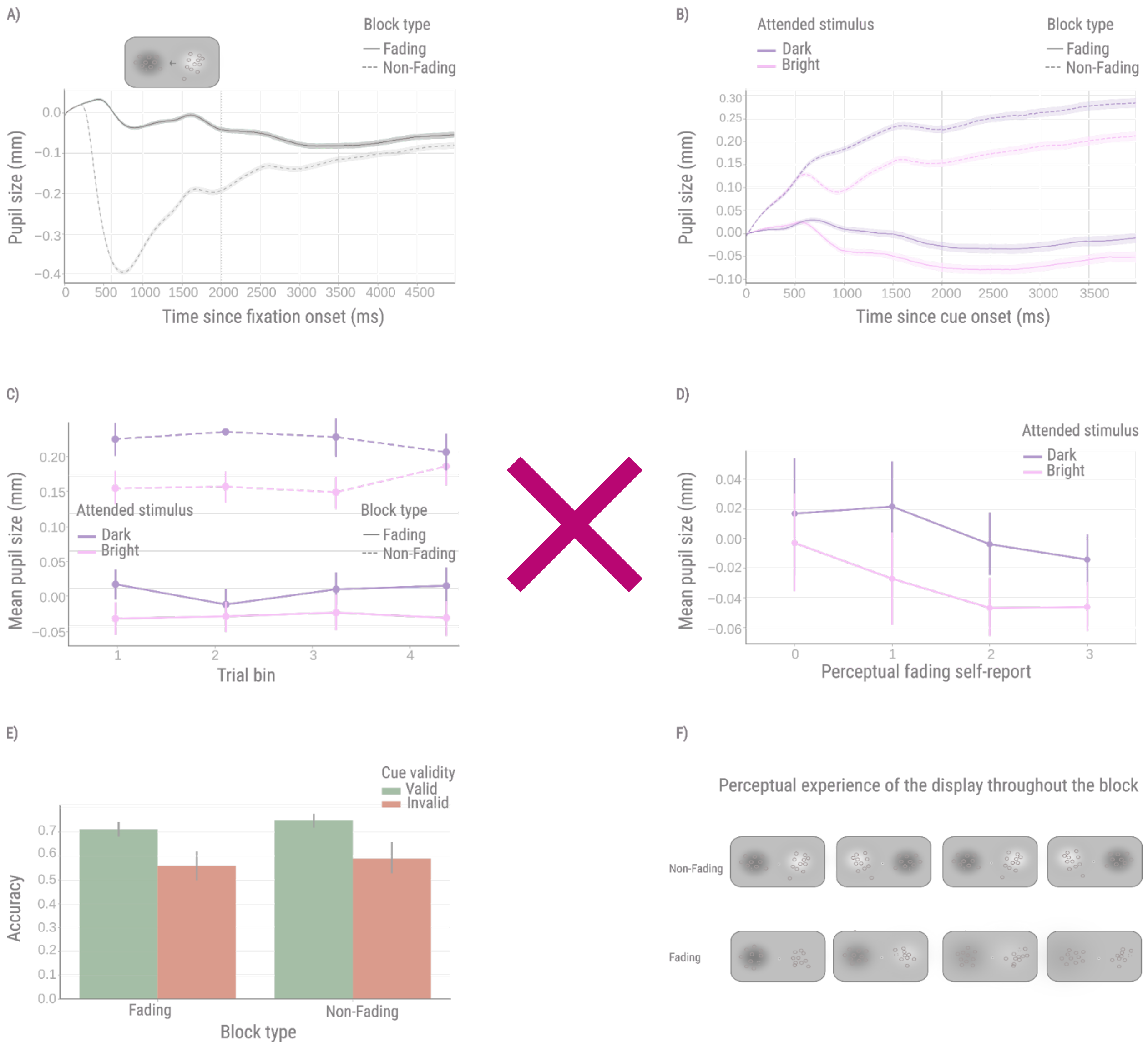
the earliest target's offset, and baselined the signal relative to 50ms after the fixation onset. For all statistical analyses, we aimed to employ a maximal random-effects structure, including by-participant random intercepts and slopes for all fixed effects and interactions. However, due to convergence issues in some cases, we had to simplify the model structure in some cases. These adjustments are transparently reported in the results section. For hypotheses that predict a null result (3.1 and 4), we also performed a Bayesian linear mixed effects model by using the "generalTestBF" function from the R-package BayesFactor (Morey, Rouder & Jamil, 2015); the models had the same fixed- and random-effects structure as the regular model, and used the corresponding dependent variables (i.e. as determined by cross-validation). Finally, to estimate the Bayes Factor (BF) of each factor, we divided the BF of the simplest model that contains a factor of interest by the BF of the same model but with that factor excluded; this approach is similar to the Inclusion Bayes Factor Based on Matched Models as implemented in Jasp and first described in Mathôt (2017), with the exception that the BF is based on a comparison of at most two models.

Results

First, we tested **Hypothesis 2** (Pupil size is smaller in the Non-Fading as compared to the Fading block) by including all trials from both blocks. The model included Pupil size (from the fixation onset until the earliest target's offset) as the dependent variable, Block type as fixed effect, and by-participant random intercepts and slopes. We found a main effect of Block type, ($z = -14.45$, $p < 0.001$, tested at 500 ms), reflecting that the overall pupil size was smaller in the Non-Fading block as compared to the Fading block. Therefore, Hypothesis 2 was confirmed (Figure 2A).

Next, we tested **Hypothesis 1** (Covert visual attention to bright/ dark modulates pupil size in the Non-Fading block) by including only the trials from the Non-Fading block. The model included Pupil size (from the cue onset until the earliest target's offset) as dependent variable, Covertly attended brightness as fixed effect, and by-participant random intercepts and slopes. We found a main effect of Covertly attended brightness, ($z = 7.25$, $p < 0.001$, tested at 1900 ms), reflecting that, in the absence of perceptual fading, pupil size was smaller when covertly attending to bright as compared to the dark stimulus. Therefore, Hypothesis 1 was confirmed (Figure 2B).

Next, we tested **Hypothesis 3** (Covert visual attention to bright/ dark does not modulate pupil size in the Fading block during full perceptual fading; Covert visual attention to bright/ dark does modulate pupil size in the Fading block during full perceptual fading, but the effect is smaller than in the Non-Fading block) by including all trials from the Non-Fading block and trials from the Fading block where participants reported high levels of adaptation (ratings of 2 and 3), to ensure full perceptual fading. The model included Pupil size (from the cue onset until the earliest target's offset) as the dependent variable, Covertly attended brightness (with Bright stimulus as a reference), Block type (with Fading block as a reference), and their interaction as fixed effects, and by-participant random intercepts. We found a main effect of Block type ($z = 20.24$, $p < 0.001$, tested at 1600, 2400, and 2600 ms), a main effect of Covertly attended brightness ($z = 6.29$, $p < 0.001$, tested at 900 ms), and an interaction effect ($z = 3.72$, $p < 0.001$, tested 900 ms). Next, we conducted corresponding Bayesian linear mixed models which revealed substantial bayesian evidence for both main effects ($BF10_{attended\_stimulus} = 3.53\times10^{32}$; $BF10_{block\_type} = 1.95\times10^{173}$) and the interaction ($BF10_{interaction} = 43.89$). These results suggest that pupil size is modulated by covert attention, also when perceptual fading occurs, but less strongly than when perceptual fading does not occur; phrased differently, perceptual fading decreases but does not eliminate the effect of covertly attended brightness on pupil size. Therefore, Hypothesis 3.2. is confirmed (Figure 2B).


A)
Block type
Fading
Non-Fading
Pupil size (mm)
0.0
−0.1
−0.2
−0.3
−0.4
0
500
1000
1500
2000
2500
3000
3500
4000
4500
Time since fixation onset (ms)
B)
Attended stimulus
Dark
Bright
Block type
Fading
Non-Fading
Pupil size (mm)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
−0.05
−0.10
0
500
1000
1500
2000
2500
3000
3500
Time since cue onset (ms)
C)
Mean pupil size (mm)
0.20
0.15
0.10
0.05
0.00
−0.05
Attended stimulus
Dark
Bright
Block type
Fading
Non-Fading
1
2
3
4
Trial bin
D)
Attended stimulus
Dark
Bright
Mean pupil size (mm)
0.04
0.02
0.00
−0.02
−0.04
−0.06
0
1
2
3
Perceptual fading self-report
E)
Cue validity
Valid
Invalid
Accuracy
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Fading
Non-Fading
Block type
F)
Perceptual experience of the display throughout the block
Non-Fading
Fading

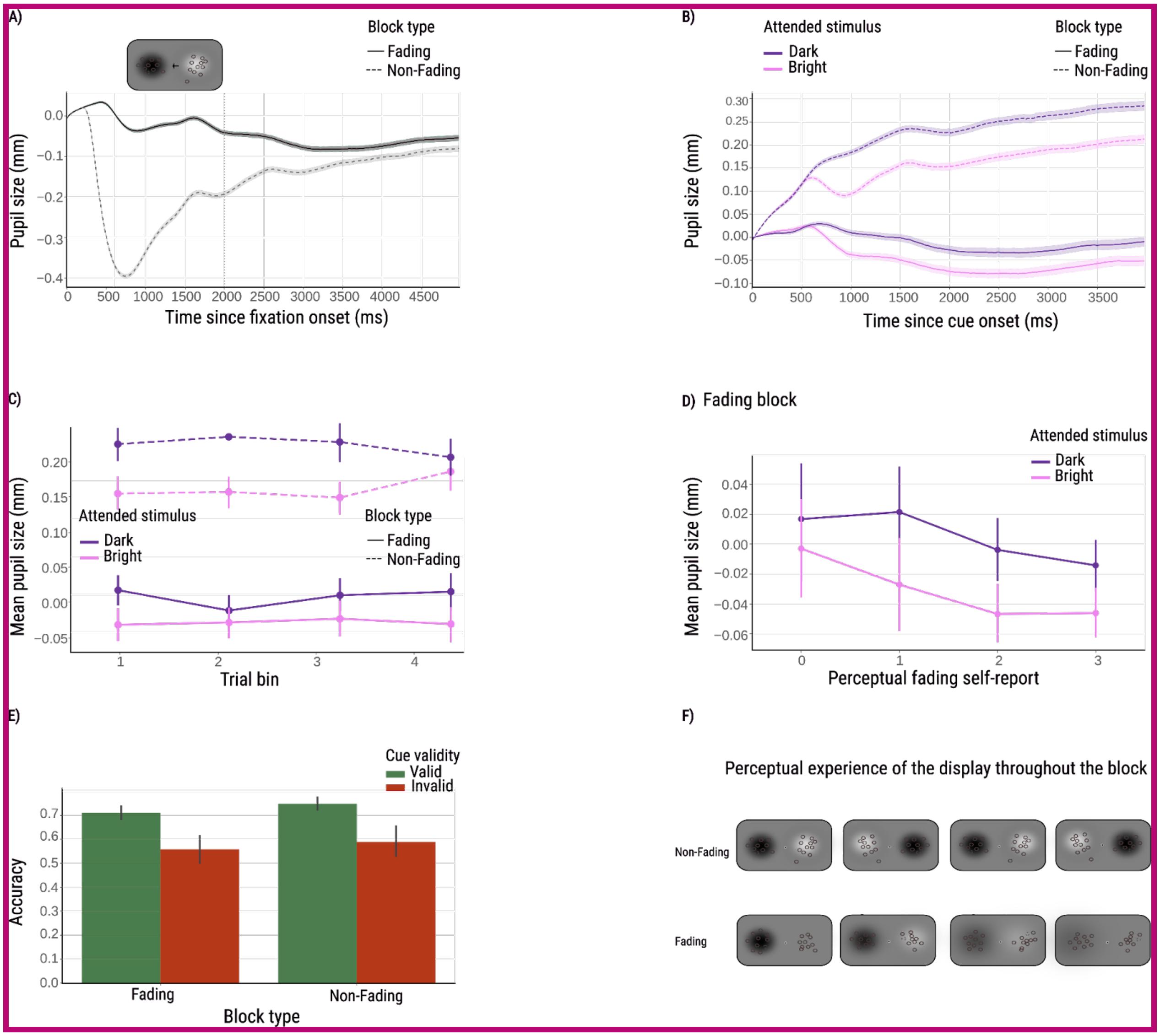


Figure 2. The pupillary (A-D) and behavioral (E) results. *A)* Pupil size is smaller in the Non-Fading as compared to the Fading block (Hypothesis 2 confirmed). *B)* Covert visual attention to bright/ dark does modulate pupil size in the Fading block during full perceptual fading, but the effect is smaller than in the Non-Fading block (Hypothesis 3.2 confirmed; Hypothesis 1 confirmed). *C)* The lack of three-way interaction between Covertly attended brightness, Trial number, and Block Type on Pupil size (Hypothesis 4 not confirmed). *D)* The lack of interaction between Covertly attended brightness and Fading self-report (Hypothesis 5 not confirmed) in the Fading block. *E)* The accuracy of responses is higher in validly cued trials compared to invalidly cued trials (Hypothesis 6 confirmed). *F)* The schematic representation of perceptual experience of the display throughout the Fading and Non-Fading block.

Next, we tested **Hypothesis 4** (The effect of covert visual attention on the pupil size decreases over time in the Fading block but not in the Non-Fading block) by including all trials. The model included Pupil size (from the cue onset until the earliest target's offset) as the dependent variable, Block type (with Fading as reference), Covertly attended brightness, Trial number, and their interactions as fixed effects, and by-participant random intercepts. This hypothesis was tested by the effect of three-way interaction between Covertly attended brightness, Trial number, and Block type on Pupil size. We did not find a three-way interaction between Covertly attended brightness, Block type, and Trial number ($z = 0.45$, $p = 0.654$, tested at 0, 1300, and 3000 ms), nor an interaction between Block Type and Covertly attended brightness ($z = 1.46$, $p = 0.142$, tested at 4000, 2900, 1900, and 2300 ms), while an interaction between Covertly attended brightness and Trial number ($z = 3.53$, $p < 0.001$, tested at 0 ms; This effect emerged almost instantaneously in this analysis because the difference between fading and non-fading blocks already emerged before the cue onset, that is, before the epoch that we used for baseline correction in this analysis) and an interaction between Block type and Covertly attended brightness ($z = 3.03$, $p = 0.002$, tested at 800 and 900 ms) were significant. In addition, and not directly relevant to the hypothesis, we found a main effect of Block type ($z = 9.57$, $p < 0.001$, tested at 2400, 3900, and 1600 ms) and a main effect of Covertly attended brightness ($z = 2.97$, $p = 0.003$, tested at 900, 1000, and 1100 ms) while a main effect of Trial number ($z = -0.47$, $p = 0.632$, tested at 3200, 1700, 3400, and 3500 ms) was not significant. Next, we conducted corresponding Bayesian linear mixed models which revealed substantial bayesian evidence for the interaction between attended stimulus and block type ($BF10_{interaction} = 97.04$) and the interaction between block type and trial number ($BF10_{interaction} = 9.11$), while there was evidence against the interaction between attended stimulus and trial number ($BF10_{interaction} =$

0.11) nor the three-way interaction between attended stimulus, block type, and trial number ($BF10_{interaction}$ = 0.08). In addition, we found substantial bayesian evidence for the main effect of attended stimulus ($BF10_{attended\_stimulus}$ = 2.24×10^{32}) and the main effect of block type ($BF10_{block\_type}$ = 8.07×10^{184}), and evidence against the main effect of trial number ($BF10_{trial\_number}$ = 0.04). Taken together, these results suggest that, regardless of perceptual fading, there were no differences in the strength of pupil size modulation by covert attention over the course of the experiment. Therefore, Hypothesis 4 was not confirmed (Figure 2C).

Next, we tested Hypothesis 5 (The effect of covert visual attention on pupil size decreases with increasing self-reported perceptual fading in the Fading block) by including the trials from the Fading block. The model included Pupil size (from the cue onset until the earliest target's offset) as the dependent variable, Covertly attended brightness, Fading self-report, and their interaction as fixed effects, and by-participant random intercepts. We did find a main effect of Covertly attended brightness (z = 3.10, p = 0.002, tested at 900 and 1000 ms), and a main effect of Fading self-report (z = -2.19, p = 0.028, tested at 3600, 2900, 3400, and 3900 ms), while the interaction (z = -0.41, p = 0.678, tested at 2000, 2900, and 300 ms) was not significant. This suggests that the effect of covert attention did not decrease as participants' perceptual fading increased. Therefore, Hypothesis 5 was not confirmed (Figure 2D).

Finally, we tested **Hypothesis 6** (The accuracy of responses is higher in validly cued trials compared to invalidly cued trials.) by including all target-offset trials. To test the behavioral cueing effect, we ran Generalized Linear Mixed Models (GLMM) twice to test a model that included Accuracy as dependent variable, Cue validity, Block type (once with Fading block as a reference, and once with Non-Fading block as a reference), and their interaction as the fixed effects, and by-participant random intercepts. We found a main effect of Cue Validity (with

Fading as a reference: $z = 5.04$, $p < 0.001$; with Non-Fading as a reference: $z = 5.20$, $p < 0.001$), while a main effect of Block Type ($z = 0.77$, $p = 0.442$) and their interaction ($z = 0.30$, $p = 0.762$) were not significant. This suggests that participants attended the cued side of the display, and did so to approximately the same extent regardless of perceptual fading. Therefore, Hypothesis 6 was confirmed (Figure 2E).

Discussion

Here we investigated whether covert visual attention to bright/ dark modulates pupil size even when subjective perceptual experience of brightness/ darkness is eliminated or strongly reduced due to perceptual fading. The present study contained two conditions: Fading and Non-Fading. In the Fading block, participants were presented with black and white patches with a fuzzy outline that were presented at the same location throughout a full block of trials, thus inducing strong perceptual fading. In contrast, in the Non-Fading block, the patches switched sides on each trial, thus preventing perceptual fading. Participants covertly attended to one of the two patches, indicated by a cue, and reported the offset of one of a set of circles that were displayed on top. We found that covert visual attention to bright/ dark does modulate pupil size even during perceptual fading (Fading condition), but to a lesser extent than when the perceptual experience of brightness/ darkness is preserved (Non-Fading condition). This implies that pupil size is always modulated by covert attention towards brightness or darkness, but that the effect decreases (without being fully eliminated) as the subjective experience of brightness or darkness decreases.

To understand the role of subjective experience of brightness/ darkness in pupil-size modulation by cognitive factors, we must address two questions. The first is whether subjective experience alone is *sufficient* to induce cognitively driven pupil-size changes. The strongest evidence supporting this comes from studies that manipulated subjective experience despite constant physical stimulation (Binda et al., 2014; Einhäuser et al., 2008; Fahle et al., 2011; Laeng & Endestad, 2012; Naber et al., 2011). As discussed earlier, Binda et al., (2014) found that when participants viewed luminance-matched naturalistic images that could either be interpreted as sun or moon, their pupils constricted more when they interpreted an image as the sun compared to when they interpreted the same image as the moon. Similarly, Naber & Nakayama, (2013) presented participants with images of the sun that were either upright or inverted. They found that when images of the sun were oriented upright, participants' pupils constricted more as compared to when the images were vertically flipped. The authors ascribed these pupil-size modulations to higher-level interpretations of image content given that low-level stimulus properties were the same. This is further supported by studies on perceptual rivalry—a phenomenon in which the same physical stimulus evokes different percepts—and binocular rivalry—a phenomenon in which each eye is presented with a different stimulus, only one of which is consciously perceived at the time. For example, Fahle et al., (2011) used binocular rivalry to present participants with two gratings of different brightness, and showed that pupil size dilates when a dark percept is dominant and constricts when a bright percept is dominant. These findings suggest that the pupil responds to perceptual interpretation rather than just the physical stimulus (Einhäuser et al., 2008; Naber et al., 2011).

The second question is whether subjective experience is *necessary* for cognitively driven pupil-size changes. This answer is less straightforward. In a study by Sperandio et al., (2018), the authors manipulated perceptual visibility by presenting images of the sun or their phase-scrambled versions to participants' left eyes, while a mask was shown to their right eyes to induce continuous flash suppression, rendering the left-eye stimuli invisible in some trials. They found that only when participants were aware of the stimuli did their pupils constrict more to images of the sun as compared to the scrambled versions. This suggests that cognitive modulations of pupil size require subjective experience of the stimuli. However, the findings of the current study indicate that, while cognitive modulations of pupil size depend to some extent on subjective experience of brightness or darkness, subjective experience is not strictly necessary. Specifically, we found that as subjective experience of brightness or darkness decreases, cognitive modulations of pupil size do diminish, but do not disappear entirely. This suggests that the influence of cognitive factors on pupil size, or at least the interaction between covert visual attention and the pupil light response, is reduced but still present even with lower levels of subjective perception.

Importantly, we found that, while the effect of covert attention on pupil size is generally reduced under conditions of perceptual fading, variability in the strength of this reduction does not seem to reflect variability in the strength of perceptual fading, regardless of whether this is measured through the passage of time or self-report. Phrased differently, attending to a bright stimulus causes your pupils to constrict less in the presence as compared to the absence of perceptual fading, but very strong perceptual fading does not seem to reduce the effect more so than relatively mild perceptual fading. One possible explanation is that high-level factors, beyond subjective perception, contributed to the persistence of the effect. Specifically, since perceptual fading is a gradual process, it is likely that participants retained prior knowledge about the location of bright or dark stimuli, and thus were aware of their presence, even if they did not fully perceive them. Thus, pupil modulation during perceptual fading may have reflected expected brightness~~, for example when making an eye movement to the dark or bright blocks~~.

Another possible explanation is that perceptual fading happens systematically and rapidly, over the course of a few trials, and subsequently stays more-or-less constant; in other words, there may not be a great deal of variability in the strength of perceptual fading from trial to trial, and consequently we cannot use this variability to predict pupil responses. Based on the present results, we cannot adjudicate between these two explanations.

Finally, the observation that the effect of covert visual attention on pupil size diminishes but does not entirely disappear during perceptual fading suggests a dual influence of high-level and low-level visual processes. On the one hand, the physical presence of stimuli—related to low-level visual processing—is important for pupil modulation. On the other hand, the subjective experience of brightness—indicative of high-level visual processing—also plays a significant role in modulating pupil size. This has important implications for understanding the origin of cognitively driven pupil-size changes. As we showed earlier, cognitively driven pupil-size changes are mediated by the image-forming pathway (Vilotijević & Mathôt, 2023). However, the present study suggests that within this pathway, both early and late levels of processing contribute to the effect. Specifically, the persistence of attention-driven effects on pupil size during fading indicates that the image-forming pathway is not completely disabled and that the brain continues to process and react to visual information, even when it is not part of conscious perception.

In sum, we showed that covert visual attention to bright/ dark does modulate pupil size even during perceptual fading, but to a lesser extent than when the perceptual experience of brightness/ darkness is preserved. In broader terms, this suggests that cognitive modulations of pupil size reflect a mixture of high-level and lower-level visual processing.

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