

The Pupillary Light Response Reflects Exogenous Attention and Inhibition of Return

Sebastiaan Mathôt¹, Edwin Dalmaijer^{2,3}, Jonathan Grainger¹, and Stefan Van der Stigchel²

¹Aix-Marseille University, CNRS, LPC UMR 7290, Marseille, France

²Dept. of Experimental Psychology, Helmholtz Institute, Utrecht University, The Netherlands

³Dept. of Experimental Psychology, University of Oxford, United Kingdom

Address for correspondence:

Aix-Marseille University, CNRS

Laboratoire de Psychologie Cognitive, UMR 7290

3 Place Victor Hugo

Centre St. Charles, Bâtiment 9, Case D

13331 Marseille

France

s.mathot@cogsci.nl

<http://www.cogsci.nl/smathot>

Abstract

Here we show that the pupillary light response reflects exogenous (involuntary) shifts of attention and inhibition of return. Participants fixated in the center of a display that was divided into a bright and a dark half. An exogenous cue attracted attention to the bright or dark side of the display. Initially, the pupil constricted when the bright, as compared to the dark side of the display was cued, reflecting a shift of attention towards the exogenous cue. Crucially, this pattern reversed about one second after cue presentation. This later-occurring, relative dilation (when the bright side was cued) reflected disengagement from the previously attended location, analogous to the behavioral phenomenon of inhibition of return. Indeed, we observed a strong correlation between ‘pupillary inhibition’ and behavioral inhibition of return. We conclude that the pupillary light response is a complex eye movement that reflects how we selectively parse and interpret visual input.

Keywords: pupillometry, visual attention, inhibition of return, eye movements

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The pupillary light response (PLR) is a well-known physiological response that is described in most neuroanatomy textbooks. What is less well known is that the PLR is not purely reflexive, as is often assumed, but is modulated by cognitive factors. For example, we and others have recently shown that the pupil constricts when you covertly (i.e. without looking at) attend to a bright stimulus, as compared to a dark stimulus (Binda, Pereverzeva, & Murray, 2013a; Mathôt, van der Linden, Grainger, & Vitu, 2013, 2014; Naber, Alvarez, & Nakayama, 2013). Moreover, stimuli that subjectively appear very bright trigger a constriction, relative to equiluminant stimuli that appear less bright (e.g., pictures of the sun vs. indoor scenes; Binda, Pereverzeva, & Murray, 2013b; Naber & Nakayama, 2013; see also Laeng & Endestad, 2012). Together, these and related findings show that the PLR is not merely a reflexive response to the amount of light that falls on the retina, but is modulated by the way in which we process and interpret visual input.

To date, studies that have investigated the link between visual attention and the PLR have focused on enhancement of the PLR by endogenous (voluntary) shifts of attention (Binda et al., 2013a; Mathôt et al., 2013; Naber et al., 2013). It has not yet been investigated whether the PLR is similarly modulated by exogenous (reflexive) shifts of attention, such as elicited by suddenly appearing stimuli. Exogenous attention provides a particularly interesting case, because (unlike endogenous attention, Chica, Klein, Rafal, & Hopfinger, 2010) it is characterized by a bi-phasic response: For a brief moment after attention is exogenously drawn to a cued location, detection and discrimination improve for stimuli presented at that location. This initial facilitation is followed by a period of inhibition (of return, IOR), during which detection and discrimination are impaired for the previously attended location (Posner & Cohen, 1984). Plausibly, IOR improves the efficiency of visual search by temporarily marking locations that have received attention and do not need to be visited again (e.g., Klein, 1988).

In the present study we investigated whether the PLR is modulated by exogenous shifts of attention, using a variation of the Posner-cuing task. Participants continuously fixated the center of a display that was divided into a bright and a dark half. A brief motion stimulus attracted

attention to the bright or dark side. We predicted that the pupil would initially constrict when attention was drawn to the bright side, relative to the dark side, reflecting attentional facilitation. We further predicted that this pattern would reverse at longer intervals after the motion stimulus, reflecting IOR.

Methods

Materials and availability

Data, materials, and analysis scripts are available from https://github.com/smathot/materials_for_P0009.1.

Participants, software, and apparatus

Seventeen naive observers (9 women; age range 19-24 years) participated in the experiment. Participants provided written informed consent. The experiment was conducted with approval of the Aix-Marseille Université ethics committee. The right eye was recorded with an EyeLink 1000 (SR Research, Mississauga, Canada, ON), a video-based eye tracker sampling at 1000 Hz. Stimuli were presented on a 21" ViewSonic pf227f CRT monitor (1024 x 768 px, 100 Hz) with OpenSesame (Mathôt, Schreij, & Theeuwes, 2012) / PsychoPy (Peirce, 2007).

Stimuli and procedure

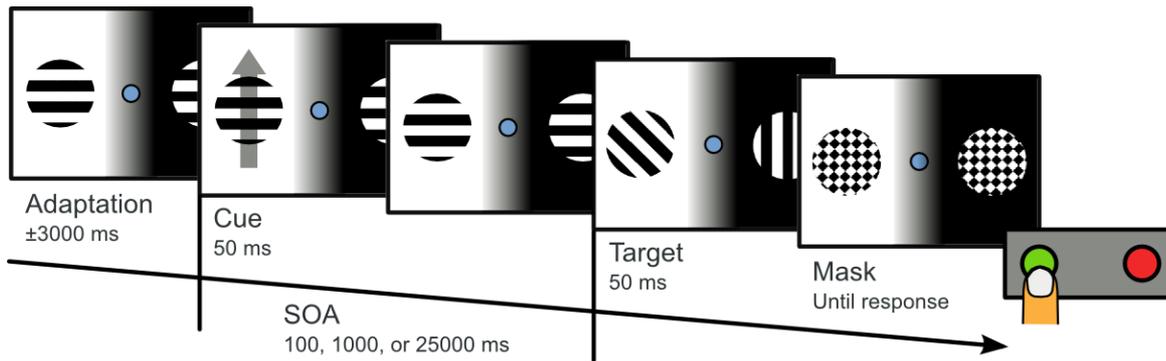


Figure 1. Schematic experimental paradigm. This example demonstrates a Valid Bright-Side-Cued trial, because the movement cue appeared on the bright side of the display and correctly predicted the location of the target. The exact duration of the adaptation period depended on the duration of the drift-correction procedure. The upwards arrow indicates the motion direction of the cue.

Before the experiment, a nine-point eye-tracker calibration was performed. At the start of the trial, the display was divided into a bright (88.5 cd/m^2) and a dark half (0.2 cd/m^2), separated by a central luminance gradient (10.0° wide). Participants were instructed to fixate a blue central fixation dot throughout the trial. Two horizontally oriented Gabor patches ($\sigma = 0.63^\circ$, $sf = 0.85$ cycles/ $^\circ$, 100% contrast, 30% opacity) were presented 10° to the left and right of the center. After an adaptation period of 1250 ms, an automatic one-point recalibration ('drift correction') was performed. From this point onwards, the luminance gradient was locked to horizontal gaze position by a continuous gaze-contingent algorithm. This ascertained that gaze was always centered exactly in between the bright and dark sides. After another adaptation period of 1250 ms, one Gabor patch (the cue) changed phase for 50 ms. This gave the appearance of a sudden upwards motion. The cue served to capture attention, but did not predict the location of the target. After a stimulus-onset asynchrony (SOA) of 100, 1000, or 2500 ms relative to cue onset, both Gabor patches changed orientation. One patch (the distractor) changed to a vertical orientation. The other patch (the target) was tilted 45° clockwise or counterclockwise from a vertical orientation. After 50 ms, both stimuli were masked with random-noise patches with the same size, average brightness, and opacity as the Gabor patches. Participants indicated the orientation of the target as quickly and accurately as possible by pressing the left (for counterclockwise) or

right (for clockwise) button on a response box. The trial ended when a button was pressed or when a timeout occurred after 3000 ms.

Cue validity (50% valid, 50% invalid), SOA (25% 100 ms, 25% 1000 ms, 50% 2500 ms), and brightness of the cued side (50% Bright, 50% Dark) were mixed within blocks. Because only the 2500 ms SOA provided a sufficiently long ‘uncontaminated’ interval for the pupil-trace analysis, this SOA occurred on half of the trials. The experiment consisted of one practice block, followed by 16 experimental blocks (512 trials), and lasted approximately two hours.

Results

Significance and trial-exclusion criteria

For the individual-differences and correlation analyses, we used a significance threshold of $p < .05$. For the linear mixed-effects (LME) analyses we used $t > 2$. This is comparable to a $p < .05$ threshold, Baayen, Davidson, & Bates (2008). However, in light of recent concerns about p-value estimation for LME models, we have omitted explicit p-values. For the pupil-trace analysis, we considered only sequences of at least 200 consecutive samples where $t > 2$ to be significant (cf. Mathôt et al., 2013). Trials were excluded when, at any point after cue onset and before feedback, participants fixated more than 2.9° from the left or right of the horizontal display center (4.9%). No other filtering criteria were applied. No participants were excluded. 8278 trials (95.1%) were entered into the analysis.

Behavioral results

We conducted an LME analysis with SOA (continuous: 100, 1000, 2500 ms) and Cue Validity (valid, invalid) as fixed effects, participant as random effect on the intercept, and accuracy as dependent measure (see Figure 2). This revealed marginal main effects of Cue Validity ($t = 1.71$) and SOA ($t = 1.51$), and a reliable Cue-Validity by SOA interaction ($t = 2.47$). The same analysis using inverse response time (1/RT) as dependent measure (we used inversion as an objective alternative to outlier removal, cf. Ratcliff, 1993) revealed a similar pattern of results: A marginal main effect of Cue Validity ($t = 1.27$), a reliable main effect of SOA ($t =$

3.68), and a reliable Cue-Validity by SOA interaction ($t = 2.51$). Separate analyses, as above but with only Cue Validity as fixed effect, showed facilitation at the 100 ms SOA (accuracy: $t = 3.20$; $1/RT$: $t = 8.67$) and IOR at the combined 1000 and 2500 ms SOAs (accuracy: $t = 2.36$; $1/RT$: $t = 2.31$). In summary, the behavioral results showed the classic bi-phasic pattern of facilitation at the short SOA, followed by IOR at longer SOAs.

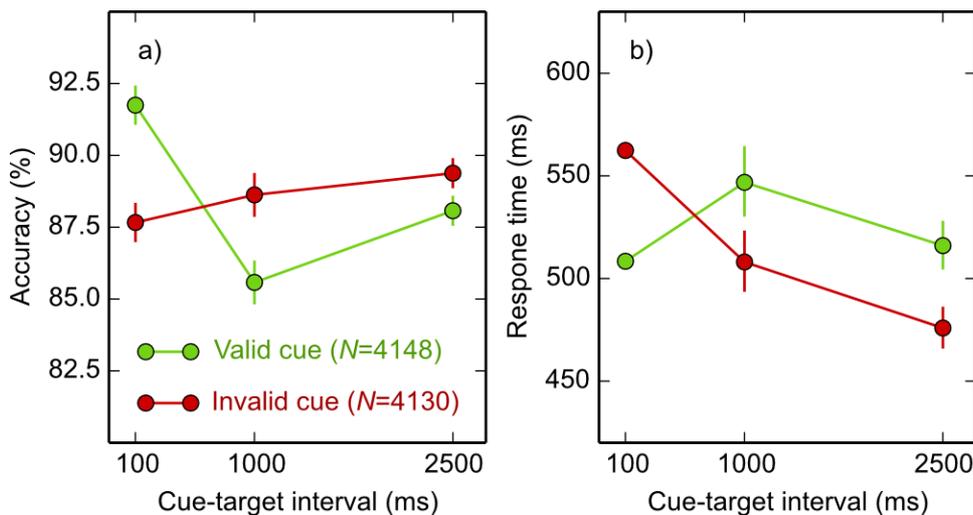


Figure 2. Accuracy (a) and response time (b) as a function of Cue Validity and SOA. Error bars indicate standard errors. Where not shown, error bars are smaller than symbols. b) Data points are based on the grand mean of the inverse response time, consistent with the analysis described in the main text.

Pupil-trace analysis

We analyzed pupil surface during the cue-target epoch, relative to a baseline period 100 ms prior to the cue onset (cf. Mathôt et al., 2013). Blinks were reconstructed using cubic-spline interpolation (Mathôt, 2013). No other filtering or smoothing procedures were applied. We analyzed only the 2500 ms SOA, which provides a large temporal window during which pupil size can be analyzed. For each 1 ms sample separately, we conducted an LME with Cued-Side-Brightness (Bright, Dark) as fixed effect, participant as random effect on the intercept, and pupil size as dependent measure.

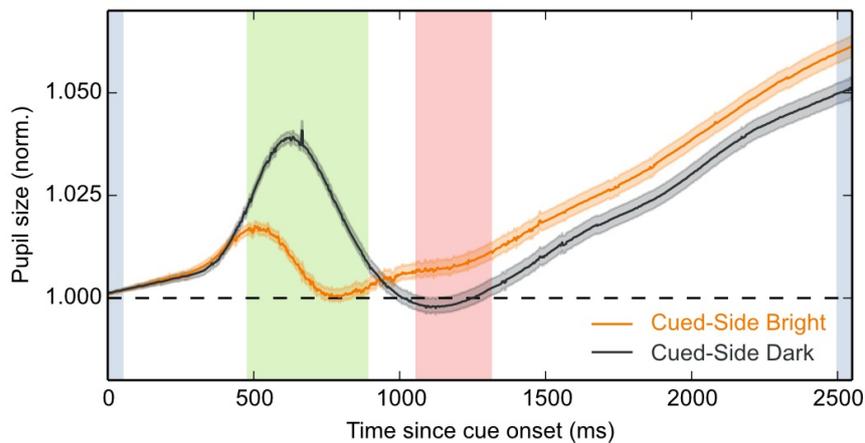


Figure 3. Pupil size as a function of Cued-Side-Brightness and time since cue onset (data from the 2500 ms SOA). Pupil size is shown as a proportion of baseline size during the 100 ms prior to cue onset. Error shadings indicate standard errors. Green shading indicates pupillary facilitation. Red shading indicates pupillary inhibition. Blue shadings indicate cue (0-50 ms) and target (2500-2550 ms) presentation. Data reflects the unsmoothed grand mean signal.

Pupil size depends on many factors other than luminance. In our data, the presentation of the cue triggered a fast, overall dilation, reflecting an orienting response (Wang, Boehnke, White, & Munoz, 2012). In addition, there was a slow dilation that persisted until the end of the trial and presumably reflected steadily increasing arousal. However, here we focus exclusively on the effect of luminance, i.e. the difference in pupil size between Cued-Side-Bright and Cued-Side-Dark trials.

As shown in Figure 3, from 476 to 893 ms after cue onset, the pupil was smaller when the bright side, relative to the dark side of the display was cued (from now on: pupillary facilitation). This effect peaked after 665 ms, and in absolute terms corresponded to a relative 2.8% pupil-area decrease (comparable to that observed for endogenous cuing, Mathôt et al., 2013). This pattern reversed significantly from 1054 to 1316 ms after cue onset (from now on: pupillary inhibition), reaching a relative peak pupil-area increase of 1.0% after 1126 ms. The reversal qualitatively persisted until the end of the trial.

Individual differences and correlation analyses

In general, there is considerable between-subject variability in IOR (e.g., Theeuwes, Mathôt, & Grainger, 2014). This was apparent in our data as well. However, rather than assume that these individual differences reflected measurement noise, we tested their reliability and used them to link pupil size to behavior.

First, to test the reliability of the individual differences, we randomly split the data in two subsets and determined the correlation between the strength of behavioral IOR in both subsets (2500 ms SOA only; ± 128 trials per participant in each subset). We repeated this procedure 10,000 times to create bootstrap estimates and 95% confidence intervals for the correlation (i.e. the split-half reliability). For behavioral IOR based on accuracy this gave $r = .71$ (.49 - .88). For behavioral IOR based on RTs this gave $r = .46$ (.02 - .79). We conducted the same analysis for pupillary inhibition, i.e. the difference in pupil size between Cued-Side-Bright and Cued-Side-Dark trials for the sample at which overall pupillary inhibition was largest (cf. Figure 4b). This gave $r = .41$ (.05 - .72).

Finally, we tested whether pupillary inhibition was related to behavioral IOR. We quantified behavioral IOR (for the 2500 ms SOA) for each participant and for both accuracy and RTs. We also quantified pupillary inhibition for each participant and for each 1 ms sample. Next, we determined correlations between pupillary inhibition and behavioral IOR, separately for accuracy and RT and for each 1 ms sample. This analysis resulted in two ‘correlation traces’, shown in Figure 4.

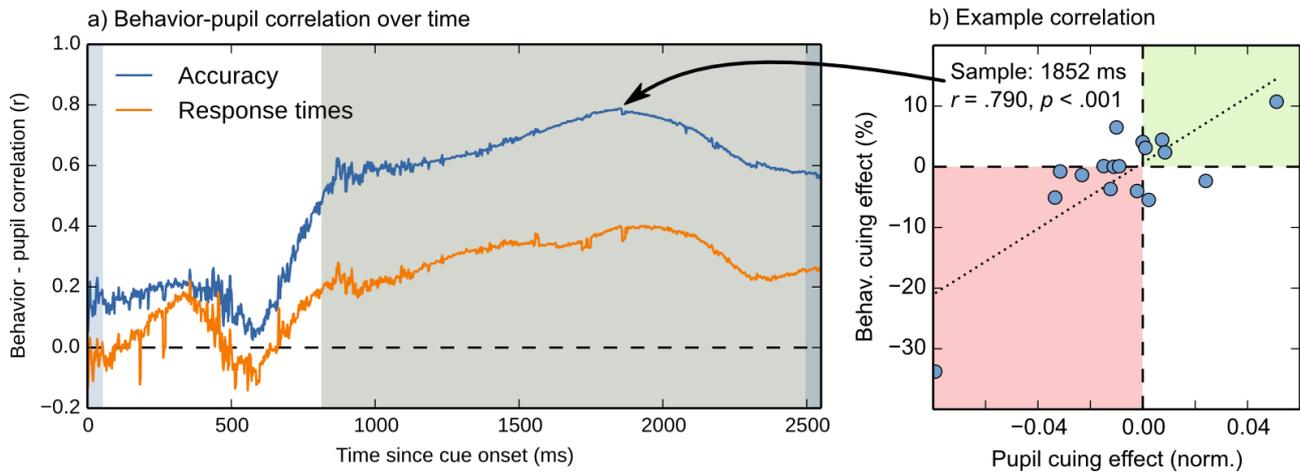


Figure 4. a) Correlation between the pupillary inhibition and behavioral IOR (based on accuracy and response times) for the 2500 ms SOA, as a function of time since cue onset. The gray shading indicates a significant correlation based on accuracy. b) Individual data points for the strongest correlation, observed for accuracy at 1852 ms post-cue. Dots in the red area indicate participants that show both pupillary inhibition and behavioral IOR. Dots in the green area indicate participants that show (sustained) pupillary facilitation and behavioral facilitation.

The correlation between pupillary inhibition and behavioral IOR based on accuracy was strong ($r > .49$) and reliable ($p < .05$) from 817 ms post-cue until target presentation, i.e. roughly during the interval at which overall pupillary inhibition was observed (Figure 4a). An identical, but weaker correlation was observed between pupillary inhibition and behavioral IOR based on RTs. (We could not use the same ‘within-SOA’ procedure to determine the correlation between pupillary and behavioral facilitation, because the 100 ms cue-target interval was too short for any pupillary effects to arise.)

To summarize, individual differences in the strength of behavioral IOR and pupillary inhibition were highly reliable. Moreover, participants who showed strong pupillary inhibition showed strong behavioral IOR, and vice versa.

Discussion

Here we report, for the first time, that the pupillary light response (PLR) reflects the focus of exogenous (reflexive) shifts of attention. When attention was drawn to a bright surface, the pupil

initially constricted, relative to when attention was drawn to a dark surface. This shows that the PLR is driven specifically by the brightness of attended stimuli, and is not a simple reflex to retinal illumination (in line with Binda et al., 2013a; Mathôt et al., 2013, 2014; Naber et al., 2013). Crucially, this effect reversed after about one second, at which point the pupil dilated when attention had been drawn to a bright, relative to a dark surface. This is analogous to the behavioral phenomenon of inhibition of return (IOR), the inhibitory phase that typically follows exogenous shifts of attention (Posner & Cohen, 1984). Individual differences revealed a strong correlation between pupillary inhibition and behavioral IOR: Participants who showed pupillary inhibition also showed behavioral IOR, and vice versa.

The present results show that the PLR is linked to visuospatial attention, and also provide a hint as to how this link may arise. We conjecture that the PLR is modulated by activity in the superior colliculus (SC), a mid-brain area that is known for its role in attention and eye movements (Awh, Armstrong, & Moore, 2006). Although the SC is not traditionally considered part of the PLR pathway, Wang et al. (2012) recently showed that microstimulation to intermediate layers of the monkey SC (SCi) triggered pupillary dilation. This dilation largely reflected an orienting response (i.e. not luminance-related and thus distinct from the PLR), but one aspect of their results suggested involvement of the PLR as well: Dilation was more pronounced when monkeys viewed dark, as compared to bright displays. One interpretation of this result is that microstimulation induced a covert shift of attention to some (unspecified) region on the display (Awh et al., 2006). Analogous to the present results, this may have triggered a pupillary constriction when the attended region was bright, relative to when it was dark.

A link between the PLR and the SCi is also supported by the fact that neurons in this area exhibit the same bi-phasic pattern of facilitation and inhibition that is observed in behavior, and that we have demonstrated here using pupillometry (Fecteau & Munoz, 2005). Neurons in the nearby superficial layers of the SC (SCs) neither show this bi-phasic response (Fecteau & Munoz, 2005), nor trigger a pupillary dilation when stimulated (Wang et al., 2012). In other words, there appears to be a highly specific link between the PLR and SCi activity. This link may play a

crucial role in modulation of the PLR by factors such as endogenous attention, mental imagery, and illusory brightness (Binda et al., 2013a, 2013b; Laeng & Endestad, 2012; Laeng & Sulutvedt, 2014; Mathôt et al., 2013, 2014; Naber & Nakayama, 2013; Naber et al., 2013).

In summary, we have shown that, after an exogenous shift of attention, the pupillary light response (PLR) exhibits the same bi-phasic pattern of facilitation followed by inhibition that is observed in behavior and neural activity. This illustrates that the PLR is not merely a low-level reflex to light, but is a complex eye movement that reflects how we selectively parse and interpret visual input.

Author contributions

All authors contributed to the study design and contributed to writing of the manuscript. SM developed the experiment and analyzed the data.

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