The pupillary light response reflects eye-movement preparation

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Abstract

When the eyes are exposed to an increased influx of light, the pupils constrict. The pupillary light response (PLR) is traditionally believed to be purely reflexive and not susceptible to cognitive influences. In contrast to this traditional view, we report here that preparation of a PLR occurs in parallel with preparation of a saccadic eye movement towards a bright (or dark) stimulus, even before the eyes set in motion. Participants fixated a central gray area and made a saccade towards a peripheral target. Using gaze-contingent display changes, we manipulated whether or not the brightness of the target background was the same during and after saccade preparation. More specifically, on some trials we changed the brightness of the target background as soon as the eyes set in motion, thus dissociating the preparatory PLR (i.e. to the brightness of the target background before the saccade) from the 'regular' PLR (i.e. to the brightness after the saccade). We show that a PLR to the brightness of the to-be-fixated target background is prepared before the eyes set in motion. This reduces the latency of the PLR by approximately 100 ms. We link our findings to the pre-saccadic shift of attention: The pupil prepares to adjusts its size to the brightness of a to-be-fixated stimulus as soon as attention covertly shifts towards that stimulus, about 100 ms before a saccade is executed. Our findings illustrate that the PLR is a dynamic movement that is tightly linked to visual attention and eye-movement preparation.

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Introduction

You need light in order to see. The more light enters the eye, the easier it is to distinguish visual signal from the intrinsic neural noise of the visual system (e.g., Burns and Baylor, 2001). Therefore, pupillary dilation improves the signal-to-noise ratio of vision, and consequently improves visual acuity, by increasing the amount of light that enters the eye. However, large pupils can also be disadvantageous, because various optical distortions are most pronounced when a large surface of the eye's lens is exposed (Denton, 1956; Campbell and Gregory, 1960). The optimal size of the pupil therefore depends on how much light is available. In darkness, visual acuity is limited by the scarcity of light, and the pupil dilates to increase light influx. In brightness, even a small pupil lets through sufficient light, and the pupil constricts to reduce optical abberations. Among other things, the pupillary light response (PLR) is therefore a mechanism to optimize visual acuity under varying levels of ambient lighting.

However, given that we make three to four eye movements per second (Rayner, 1998), the PLR, which has a latency of 250 - 500 ms (Ellis, 1981), would seem to be too slow to serve its presumed function. When you make an eye movement towards a bright object, your pupil would seem to constrict only after your gaze has already shifted elsewhere.

Here we test the hypothesis that preparation is an important characteristic of the PLR. When you prepare a saccadic eye movement towards a stimulus, a PLR to that stimulus' brightness is prepared already before the eyes set in motion, during preparation of the saccade itself. Preparation could allow the visual system to rapidly track changes in brightness of visual input, despite the fact that the PLR is a relatively slow response.

There are two main findings that support this hypothesis. Firstly, every saccade is preceded by a covert shift of attention (Kowler et al., 1995; Deubel and Schneider, 1996): If you prepare a saccade towards a stimulus, you will start to perceive that stimulus more clearly sometime before the saccade is executed. Secondly, we and others have recently shown that a PLR is elicited by a covert shift of attention (Binda et al., 2013a; Mathôt et al., 2013; Naber et al., 2013). In our experiment, participants continuously fixated on the center of a display that was divided into a bright and a dark half (Mathôt et al., 2013). Participants identified a target stimulus that was presented on the bright or dark background. The target's probable location was indicated by

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a cue, which induced a covert shift of attention to the cued side. Crucially, the pupil constricted when attention was directed to the bright, as compared to the dark side of the display. This showed that a PLR is elicited by a covertly attended stimulus, even when eye position and visual input are controlled for.

In sum, saccadic eye movements are preceded by covert shifts of attention (Kowler et al., 1995; Deubel and Schneider, 1996), and covert shifts of attention elicit a PLR (Binda et al., 2013a; Mathôt et al., 2013; Naber et al., 2013). Here we combine these findings and show that a PLR is prepared simultaneously with the preparation of a saccade towards a bright (or dark) stimulus.

Methods

Materials and availability

Experimental scripts, participant data, analysis scripts, and supplementary control analyses are available from the first author's website, or from https://github.com/smathot/materials_for_P0001.

Participants and ethics statement

Eight observers (six naive participants and two authors; seven women; age range 20-30 years) participated in the experiment. Participants were recruited through the participant pool of Aix-Marseille Université (AMU), and provided written informed consent. The experiment was conducted with approval of the AMU ethics committee.

Software and apparatus

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" CRT monitor (1024 x 768 px, 100 Hz). Stimuli were presented with OpenSesame (Mathôt et al., 2012) using the PsychoPy back-end (Peirce, 2007).

Stimuli, task, and design

Before the experiment, a nine-point eye-tracker calibration was performed. Before each trial, a single-point re-calibration was performed ('drift correction').

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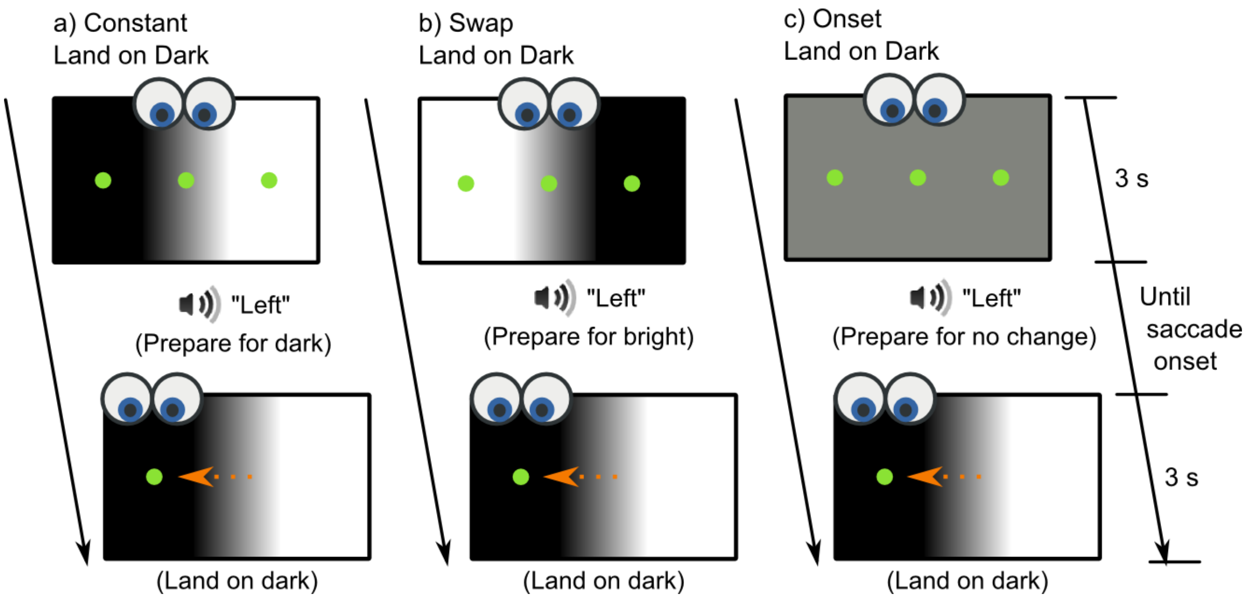

Figure 1. *Schematic experimental paradigm. a) An example of a Land-on-Dark Constant trial, in which the pupil prepares for, and lands on, a dark target background. b) An example of a Land-on-Dark Swap trial, in which the pupil prepares for brightness, but lands on darkness. c) An example of a Land-on-Dark Onset trial, in which the pupil prepares for an intermediate (unchanged) luminance, but lands on darkness. The display change occurred as soon as the onset of a saccade was detected.*

Each trial started with the presentation of three dim green dots (14.7 cd/m^2; 0.1°), presented at the display center and 10.0° degrees to the right and left of the center (see Figure 1). Participants fixated on the central dot. In the Constant and Swap conditions, the background was divided into a bright (88.5 cd/m^2) and a dark (0.2 cd/m^2) half, separated by a central luminance-gradient band (10.0° wide). In the Onset condition, the background was uniformly gray (20.8 cd/m^2). After 3 s, a voice saying *gauche* (left) or *droite* (right) was played back through a set of speakers, instructing participants to make a saccade to the left or right dot. Saccades were detected on-line as the moment at which horizontal gaze position deviated more than 2.9° from the central dot for at least two consecutive gaze samples. (For analysis and verification we used an off-line detection algorithm, described under Off-line saccade detection.) The target dot remained visible throughout the trial. The central and non-target dots were removed on saccade detection.

As soon as a saccade was detected, one of three things could happen. In the Constant condition, the display did not change at all (Figure 1a). Therefore, pre-saccadic preparation of

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the PLR should result in a reduction of the PLR latency. In the Swap condition, the dark side of the screen turned bright and vice versa (Figure 1b). Therefore, pre-saccadic preparation should result in a brief ‘inverse’ PLR, reflecting the PLR’s preparatory component. In the Onset condition, the uniformly gray display was divided into a bright and a dark half (Figure 1c). In this condition, there could be no pre-saccadic preparation of the PLR, because the central dot and the saccade target were (initially) on the same gray background. The trial ended 3 s after saccade detection.

In sum, we used a fully crossed 2 x 3 design. The first factor, Landing Luminance (Land on Bright or Land on Dark), corresponded to the post-saccadic luminance of the target background. The second factor was Condition (Constant, Swap, or Onset). Both factors were randomly mixed within blocks. Saccade direction (Left or Right) was fully randomized. The experiment consisted of 360 trials across ten blocks, and lasted approximately 90 minutes.

Pupil-trace analysis

Each trial was divided into three epochs: the baseline epoch, spanning the 100 ms prior to the presentation of the auditory cue; the pre-saccade epoch, from the cue until the detection of the saccade; and the post-saccade epoch, from the detection of the saccade until the end of the trial. We analyzed pupil surface relative to the mean pupil size during the baseline epoch (cf. Mathôt et al., 2013). Missing data during blinks was reconstructed, where possible, using cubic-spline interpolation (Mathôt, 2013). No signal smoothing was applied.

Trial-exclusion criteria

Trials were excluded based on the following criteria: A saccade was executed in the wrong direction or before the auditory cue was presented (8.4%); Saccade latency was less than 50 ms or more than 2000 ms (0.5%); The display change did not occur during the saccade, as determined by off-line verification of saccade detection (4.9%; See Off-line saccade detection); Blinks occurred and could not be reconstructed (4.5%, see Pupil-trace analysis). After exclusion, 2350 trials (81.4%) remained for further analysis.

Off-line saccade detection

For the analysis, we used the EyeLink saccade-detection algorithm (velocity threshold: 35 °/s;

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acceleration threshold: 9500 °/s^2). For each trial, we considered the first saccade that was larger than 1.8°. Saccades were executed on average 543.6 ms (*SD* = 187.4) after the auditory cue, with considerable variation between participants (409 - 789 ms; participant means). The fact that saccades were relatively slow is presumably due to the instruction's emphasis on accuracy, the low visibility of the saccade target, and the use of an endogenous auditory cue.

Immediately after the display change, a trigger was sent to the eye tracker to allow off-line verification of timing. This showed that the display change occurred exactly in the middle of the saccade, 27.09 ms (*SD* = 3.906) after saccade onset and 27.55 ms (*SD* = 7.852) before saccade offset. The average saccade duration was 54.63 ms (*SD* = 7.407). All trials in which the display change did not occur during the saccade were discarded (see also Trial-exclusion criteria).

Results

The PLR is affected by the luminance of the pre-saccadic target background

The main results are shown in Figure 2a, in which the difference in pupil size between Land-on-Bright and Land-on-Dark trials is plotted over time. The PLR, which is a relative constriction on Land-on-Bright trials and shown as a negativity in the figure, is present in all conditions.

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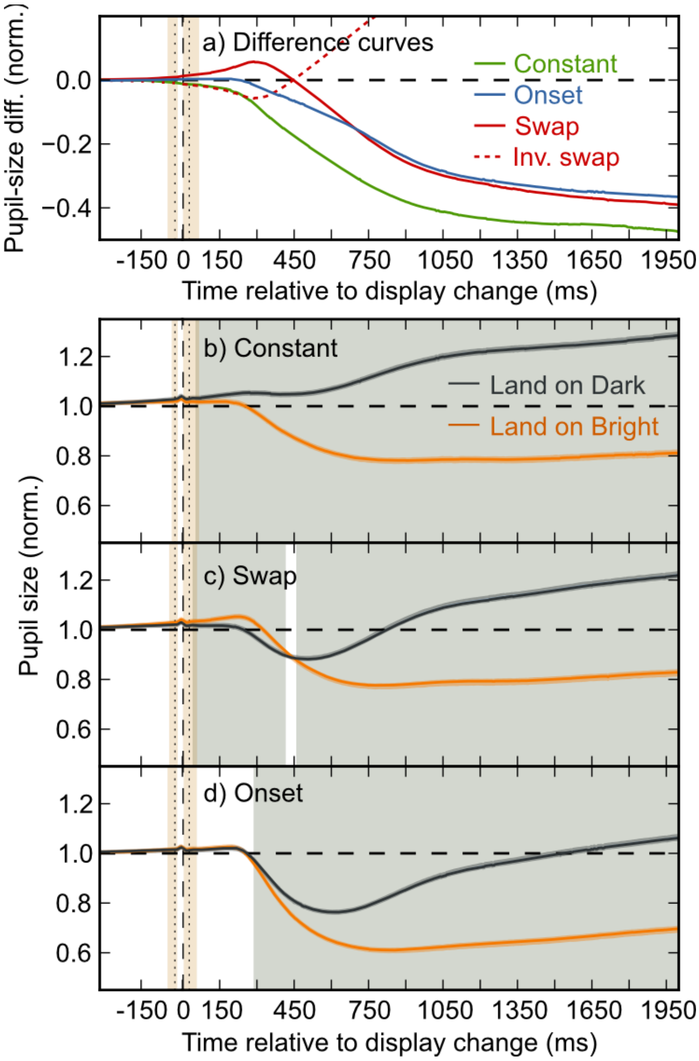

Figure 2. *a) Mean difference in pupil size between Land-on-Bright and Land-on-Dark trials for the three conditions (solid lines) as a function of time relative to display change. The PLR is shown as a negativity. The red dotted line shows the inverse of the Swap condition, and is shown for comparison with the Constant condition. b, c, d) Mean pupil size on Land-on-Dark and Land-on-Bright trials over time for the Constant (b), Swap (c), and Onset (d) conditions. The PLR is shown as a decreased pupil size on Land-on-Bright trials, relative to Land-on-Dark trials. Line widths indicate 95% confidence intervals, such that non-overlapping lines correspond to $p < .05$. Gray background shadings indicate significant ($p < .05$)*

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divergence between Land-on-Dark and Land-on-Bright trials for at least 200 consecutive samples. a, b, c, d) The vertical dotted lines correspond to mean saccade onset (left-most) and offset (right-most). The surrounding shadings indicate the full range of observed values. The display change (or a dummy change in the Constant condition) occurred at time 0, indicated by the dashed vertical line.

To determine at which points in time there was a significant difference in pupil size between Land-on-Bright and Land-on-Dark trials we conducted linear mixed-effects (LME) analyses with Participant as random effect, Target Luminance (post-saccadic; Land-on-Dark or Land-on-Bright) as fixed effect, and Pupil Size as dependent measure. This analysis was performed separately for each time point and condition. Markov chain Monte Carlo (MCMC) simulation was used to estimate *p* values and 95% confidence intervals (Baayen et al., 2008). We considered divergence between Land-on-Dark and Land-on-Bright trials to be significant when $p < .05$ for at least 200 consecutive samples (cf. Mathôt et al., 2013).

Preparation of the PLR was evident in two main ways. Firstly, divergence occurred much earlier in the Constant condition (from 58 ms after display change until trial end) than in the Onset condition (292 ms - trial end). Since the latency of the PLR is at least 250 ms (Ellis, 1981), this extremely rapid modulation of pupil size clearly shows that a PLR was prepared before the saccade was initiated.

Secondly, in the Swap condition there was initially an 'inverse PLR', again arising very rapidly (46 - 411 ms). This reflects a preparatory response to the pre-saccadic brightness of the target background, before the display had changed (Figure 1b). Strikingly, the (inverse of the) Swap condition was indistinguishable from the Constant condition until about 250 ms after the saccade (compare the dotted-red and green lines in Figure 2a). This suggests that it takes about 250 ms for the pupil to respond to the post-saccadic luminance, which is roughly consistent with the latency of the PLR in the Onset condition (292 ms, see above) as well as previous estimates of the PLR latency (e.g., Ellis, 1981). From about 600 ms onwards the Swap condition was indistinguishable from the Onset condition (compare the solid-red and blue lines in Figure 2a),

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suggesting that by this time the preparatory component of the PLR had fully dissipated. Crucially, the results from the Swap condition show that when you prepare an eye movement towards a stimulus on a bright (or dark) background, a preparatory PLR is (partly) elicited even when the luminance of the target background is changed before the target is brought into central vision.

Modeling the PLR using exponential decay

In order to further characterize the difference between Constant and Onset trials, we modeled the shape of the PLR using an exponential-decay function. This modeling approach complements the LME analysis described above in two important ways.

Firstly, the LME analysis simply takes the first point in time at which there is significant divergence between Land-on-bright and Land-on-Dark trials as the onset of the PLR. However, a visual inspection of Figure 2a suggests that preparation does not merely reduce the latency of the PLR, but qualitatively alters the shape of the PLR. More specifically, if preparation was possible (i.e. in the Constant condition), the PLR appeared to consist of a small initial bias, followed later by a much larger response, which we will call the 'full PLR' from now on. An important question is whether the effect of preparation is limited to this initial bias, or whether the latency of the full PLR is reduced as well.

Secondly, modeling exposes trivial differences between conditions, notably differences in noise level and response size. This is important, because larger and less noisy responses may seem to occur earlier when using significance testing (e.g., LME).

In a pilot study, we compared a number of decay functions and found that, given the right parameters, several functions fit the PLR (and the difference in pupil size between Land-on-Bright and Land-on-Dark trials, which we model here) very well. Here we chose an exponential-decay function, adapted from Hoeks and Levelt (1993), which models the difference in pupil size between Land-on-Bright and Land-on-Dark trials (`p(t)`) as a function of time since display change (`t`; see Figure 3). The advantage of exponential-decay over other functions that we considered is that its parameters have clear interpretations: full PLR latency (`t0`), initial pupil-size difference (`p1`), final pupil-size difference (`p2`), and response speed (the inverse of `s`).

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Because the Swap condition is a combination of two opposite responses (to the pre- and post-saccadic brightness of the target, see Figure 2c), it is not properly modeled by exponential decay. Therefore, we model only the Constant and Onset conditions.

$$where \quad t \geq t_0 : p(t) = e^{\frac{-t+t_0}{s}} \cdot (p_1 - p_2) + p_2$$
$$where \quad t < t_0 : p(t) = p_1$$

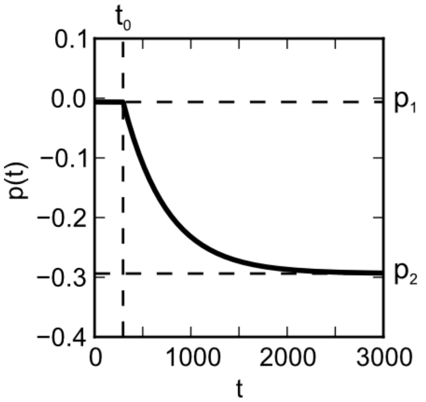

Figure 3. *We used an exponential-decay function to model the difference in pupil-size between Land-on-Bright and Land-on-Dark trials (p(t)) as a function of time since display change (t). This function has four free parameters: full PLR latency (t0), initial pupil-size difference (p1), final pupil-size difference (p2), and response speed (the inverse of s).*

For each participant separately, we determined the model parameters for the mean difference response in the Constant and Onset conditions (Figure 4). Next, we used paired-samples *t* tests to test for differences between model parameters, using a Bonferroni-corrected alpha level of .0125 (= .05 / 4 comparisons).

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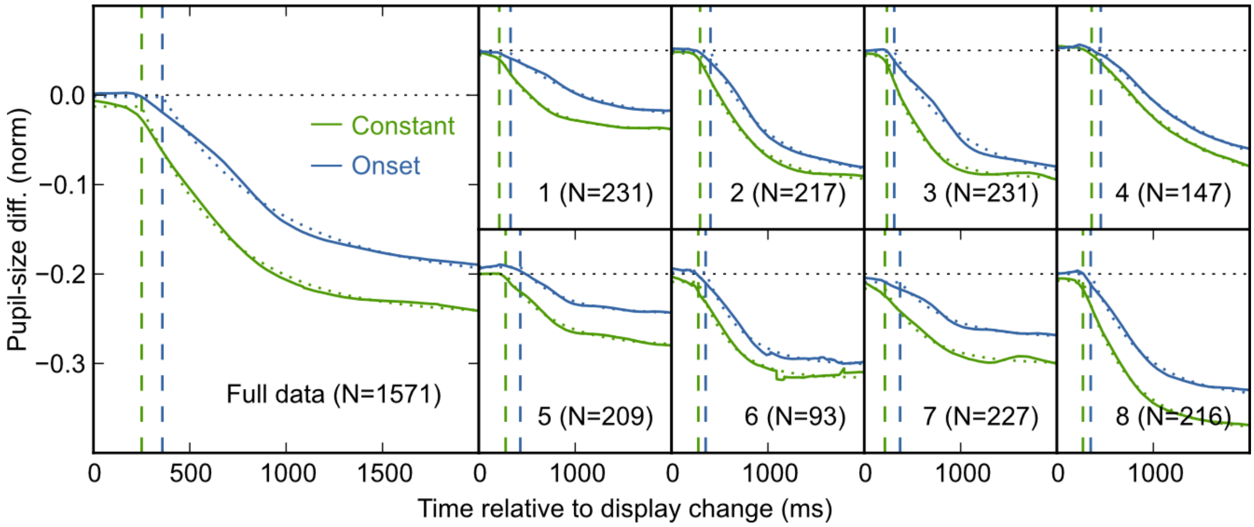

Figure 4. *Observed difference in pupil size between Land-on-Bright and Land-on-Dark trials (solid lines) and model fits (dotted lines) for the Constant and Onset conditions. Vertical dashed lines indicate full PLR latencies (`t0`). The left pane depicts the grand mean response. The eight rightward panes show the mean responses for each of the eight participants.*

Firstly and most importantly, full PLR latency (`t0`) was 107 ms lower on Constant trials (*M* = 268, *SE* = 16.0) than on Onset trials (*M* = 375, *SE* = 16.6, $t(7) = 9.33$, $p < 0.0001$). In addition, initial pupil-size difference (`p1`) was slightly smaller (i.e. more negative) on Constant (*M* = -0.0110, *SE* = 0.0038) than on Onset trials (*M* = -0.0004, *SE* = 0.0032, $t(7) = 4.17$, $p = .0042$), as was final pupil-size difference (`p2`; Constant: *M* = -0.2542, *SE* = 0.0236; Onset: *M* = -0.2187, *SE* = 0.0268; $t(7) = 3.56$, $p = .0093$). Response speed was slightly higher (i.e. a lower `s`) in the Constant condition (*M* = 491.3, *SE* = 79.64) than in the Onset condition (*M* = 623.5, *SE* = 83.96), but this difference was not significant ($t(7) = 2.295$, $p = .0554$).

In sum, the exponential-decay model allowed us to disentangle the initial bias in the PLR (`p1`), which is only observed when preparation is possible (i.e. in the Constant condition), from the full PLR, which has a reduced latency (`t0`) when preparation is possible (i.e. in the Constant condition relative to the Onset condition). This corroborates and extends the LME analysis, which did not distinguish between these two different components of the preparatory PLR.

Discussion

Here we report, for the first time, that the pupillary light response (PLR) is partly preparatory.

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When you prepare a saccadic eye movement towards a bright (or dark) stimulus, the pupil prepares to adjust its size to the impending luminance change already before the eyes set in motion. This finding contrasts with the traditional view that the PLR is a low-level reflex to light, and shows that the PLR is tightly linked to visual attention and eye movements (see also Binda et al., 2013a; Mathôt et al., 2013; Naber et al., 2013).

Preparation has two more-or-less distinct effects on the PLR. Firstly, when preparation was possible, we observed that pupil size was affected almost instantaneously by the luminance of a newly fixated surface, within 50 ms after saccade offset (Figure 2b). Given that it takes 250 to 500 ms for the pupil to respond to luminance changes (Ellis, 1981), this initial response must result from preparation. This initial response, which is small, is followed some time later by a more much pronounced response, which we have called the 'full PLR'. Preparation reduces the latency of the full PLR by about 100 ms (based on model estimates of `t0`, shown in Figure 4). This latency reduction closely matches the finding that a covert shift of attention precedes every saccade by approximately 100 ms (Deubel, 2008; Rolfs and Carrasco, 2012). We suggest that the pre-saccadic shift of attention drives the preparatory PLR, and that the pupil prepares to adjust its size at the moment that attention covertly shifts towards the target of an upcoming saccade.

The effect of preparation was particularly striking when a saccade was prepared towards a bright (or dark) stimulus that was changed before being brought into central vision. More specifically, in the Swap condition (Figure 2c), the brightness of the display reversed polarity as soon as a saccade was detected. Consequently, when preparing a saccade towards a bright target, the eyes landed on a dark target, and vice versa. Our crucial finding is that the pupil initially responded to the pre-saccadic brightness of the target. Again, this initial response occurred almost immediately after the eye movement (±19 ms after saccade offset), suggesting that it is entirely preparatory.

Our results complement recent studies that have demonstrated high-level effects on the PLR. Most relevant here is the recent finding that the PLR is modulated by covert visual attention (Binda et al., 2013a; Mathôt et al., 2013; Naber et al., 2013): Merely attending to a bright stimulus from the corner of your eye triggers a pupillary constriction. Another striking result, which dates back almost a century, but has recently been re-discovered, comes from binocular

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rivalry. In these studies, stimuli of different brightness are presented to each eye (e.g., Harms, 1937; Fahle et al., 2011; Naber et al., 2011). The crucial finding is that the pupil constricts when the brighter stimulus dominates awareness, relative to when the darker stimulus dominates. This shows that the PLR reflects visual awareness, rather than objective luminance. A related finding is that the pupil constricts when viewing images that are interpreted as very bright, such as pictures of the sun, compared to equiluminant control images (Laeng and Endestad, 2012; Binda et al., 2013b; Naber and Nakayama, 2013). Finally, and perhaps most strikingly, merely thinking about a bright stimulus induces a pupillary constriction (Laeng and Sulutvedt, 2014). Taken together, these very different studies converge on a very similar conclusion: The PLR is not just a reflexive response to light, but reflects what we (covertly) attend to, what we are aware of, how we interpret visual input, and even what we think about. Our study complements these findings by showing that the PLR is linked to saccade preparation. Functionally, the preparatory PLR may allow the visual system to track the rapid changes in input brightness that result from saccadic eye movements.

It is an appealing conjecture that the preparatory PLR reflects pre-saccadic neural activity in the superior colliculus (SC), a midbrain structure involved in both saccade generation (Robinson, 1972) and pupillary responses (Wang et al., 2012). Many SC neurons exhibit a gradual build-up of activity that reflects the initial stage of saccade preparation (Munoz and Wurtz, 1995). This build-up activity may be related to the very early, small effect of luminance on pupil size that we observed here. Build-up activity is followed by a vigorous burst of neural activity, which is directly related to saccade execution and may have triggered the 'full' preparatory PLR that we observed here. Although the link between our results and saccade-related SC activity is clearly speculative, these and other hypotheses could be tested by comparing the preparatory PLR for pro-, anti-, and memory-guided saccades, which are associated with particular patterns of SC activity (e.g., Munoz and Wurtz, 1995; Everling et al., 1999). Therefore, we believe that pupillometry is a powerful new tool to investigate the dynamics of saccade preparation.

In conclusion, we have shown that the pupil prepares for the brightness of stimuli before they are brought into central vision. We have suggested that this finding is linked to the pre-saccadic shift of attention (Kowler et al., 1995; Deubel and Schneider, 1996): The pupil prepares a light response as soon as attention shifts towards the target of an upcoming saccadic eye movement.

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