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 during the saccade, 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 preparation triggers a pupillary response to the brightness of a to-be-fixated target background already before the eyes have landed on it. We link our findings to the pre-saccadic shift of attention: The pupil prepares to adjust its size to the brightness of a to-be-fixated stimulus as soon as attention covertly shifts towards that stimulus. 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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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 & 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 (Campbell & Gregory, 1960; Denton, 1956). Therefore, the optimal size of the pupil 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 (see Woodhouse & Campbell, 1975 for a discussion), the pupillary light response (PLR) is therefore a mechanism to optimize visual acuity under varying levels of ambient lighting.

However, given that you make three to four eye movements per second (Rayner, 1998), the PLR, which has a latency of 220 - 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 property 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 (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995): 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 covert shift of attention elicits a PLR (Binda, Pereverzeva, & Murray, 2013a; Mathôt,

Dalmaijer, Grainger, & Van der Stigchel, 2014; Mathôt, van der Linden, Grainger, & Vitu, 2013; Naber, Alvarez, & Nakayama, 2013). In one of our studies, 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 a cue, which caused participants to direct their attention towards 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 (Deubel & Schneider, 1996; Kowler et al., 1995), 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

Participants, software, and apparatus

Eight observers (six naive participants and two authors; seven women; age range 20-30 years) participated in the experiment. Participants provided written informed consent. The experiment was conducted with approval of the *Comité d'Ethique de l'Université de Provence* (currently Aix-Marseille University). 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) using the PsychoPy (Peirce, 2007) back-end. An on-line supplement with additional analyses is available from the publisher's website. Data, experimental scripts, and analysis scripts are available from https://github.com/smathot/materials_for_P0001.

Stimuli and procedure

Before the experiment, a nine-point eye-tracker calibration was performed. Before each trial, a single-point re-calibration ('drift correction') was performed.
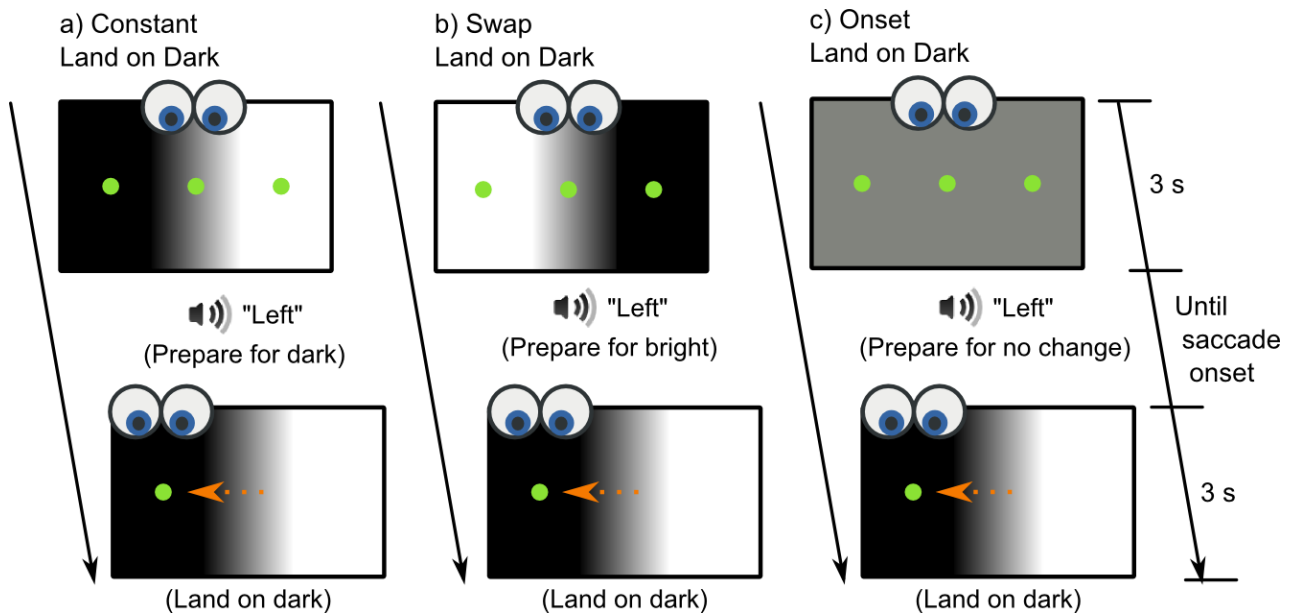
Figure 1. *Schematic experimental paradigm. a) An example of a Land-on-Dark Constant trial, in which the pupil prepares for, and lands on, a dark target background. b) An example of a Land-on-Dark Swap trial, in which the pupil prepares for brightness, but lands on darkness. c) An example of a Land-on-Dark Onset trial, in which the pupil prepares for an intermediate (unchanged) luminance, but lands on darkness. The display change occurred during the saccade.*

Each trial started with the presentation of three dim green dots (14.7 cd/m^2; 0.1°) at the display center and 10.0° 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 (10.0° wide). In the Onset condition, the background was uniformly gray (20.8 cd/m^2). After 3 s, an auditory cue, *gauche* (left) or *droite* (right), instructed a leftwards or rightwards saccade. Saccades were detected on-line when horizontal gaze position deviated more than 2.9° from the central dot for at least two consecutive gaze samples. The target dot remained visible throughout the trial. The central and non-target dots were removed when a saccade was detected. Participants were instructed to maintain fixation on the target dot until the end of the trial.

Upon saccade detection, one of three things happened. In the Constant condition, the display did not change (Figure 1a). Therefore, pre-saccadic preparation should result in a reduction of PLR latency. In the Swap condition, the dark side of the screen turned bright and vice versa (Figure 1b). Therefore, preparation should result in a brief (seemingly) 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, preparation was impossible (or, rather, there was preparation for no change), because the central dot and the saccade target were (initially) on the same gray background. The trial ended 3 s after saccade detection.

Landing luminance (Land-on-bright, Land-on-Dark) and Condition (Constant, Swap, Onset) were equiprobable and randomly mixed within blocks. Saccade direction (Left, Right) was fully randomized. The experiment consisted of 360 trials across 10 blocks, and lasted approximately 90 minutes.

Attributing pupillary responses to preparation

There is a considerable delay between the moment that preparation of a PLR starts, and the moment that the iris muscles set in motion to change the size of the pupil. Because of this delay, even when preparation starts before saccade execution, the first pupil-size changes may occur only during or after the saccade. Therefore, we need a criterion to unambiguously attribute pupillary responses to pre-saccadic preparation, even if these pupillary responses occur during or after the saccade. More specifically, we need to know the first moment at which the pupil could, in theory, respond to events that occurred at the time of the saccade. This is important in our experiment, because our conditions differ in the display change that occurs during the saccade, which could lead to differences in the overall shape of the pupillary response between the Onset, Constant, and Swap conditions (e.g., Barbur, Harlow, & Sahraie, 1992). (Our main analyses focus on the differences between Land-on-Dark and Land-on-Bright trials within conditions, which are equal in terms of visual change.) A lower bound for the pupillary response latency is 220 ms (Ellis, 1981; visual change triggers a much slower response, Gamlin, Zhang, Harlow, & Barbur,

1998). Thus, we consider the first 220 ms after the display change to reflect preparatory activity.

Data analysis and selection criteria

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, or until another saccade was made (i.e. when participants broke fixation before 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.

For the analysis, we used the EyeLink saccade-detection algorithm (velocity threshold: 35 °/s; acceleration threshold: 9500 °/s^2), and 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. Off-line verification of timing, based on a trigger that was sent to the eye tracker immediately after the display change, showed that the display change occurred 27.09 ms (SD = 3.906) after saccade onset and 27.55 ms (SD = 7.852) before saccade offset. In other words, the display change fully occurred during the saccade, even allowing for the monitor's phosphor persistence (< 10 ms, P. Wang & Nikolic, 2011) and refresh cycle.

Trials were excluded when saccades were executed before the cue or in the wrong direction (8.4%), when saccade latency was less than 50 ms or more than 2000 ms (0.5%), when the display change did not occur during the saccade (4.9%; per off-line verification), or when blinks occurred and could not be reconstructed (4.5%). A total of 2350 trials (81.4%) remained for further analysis. There were no notable condition differences in saccade size (Constant: 9.74°, Onset: 9.51°, Swap: 9.70°), proportion of discarded trials (Constant: 18.5%, Onset: 17.8%, Swap: 18.9%), or fixation stability during the post-saccade epoch (mean standard deviation of horizontal gaze position; Constant: 0.28°, Onset: 0.35°, Swap: 0.31°).

<div align="center">Results</div>

The effect of eye-movement preparation on the PLR

Pupil size depends on numerous factors (see Laeng, Sirois, & Gredebäck, 2012 for a review), but here we focus on the effect of target-background luminance within conditions (i.e. the PLR). The PLR corresponds to a negativity in Figure 2a, and a constriction on Land-on-Bright trials, relative to Land-on-Dark trials in Figure 2b,c,d. The interval up to 220 ms after the display change is crucial, because we predicted a luminance effect during this interval if, and only if, preparation was possible.
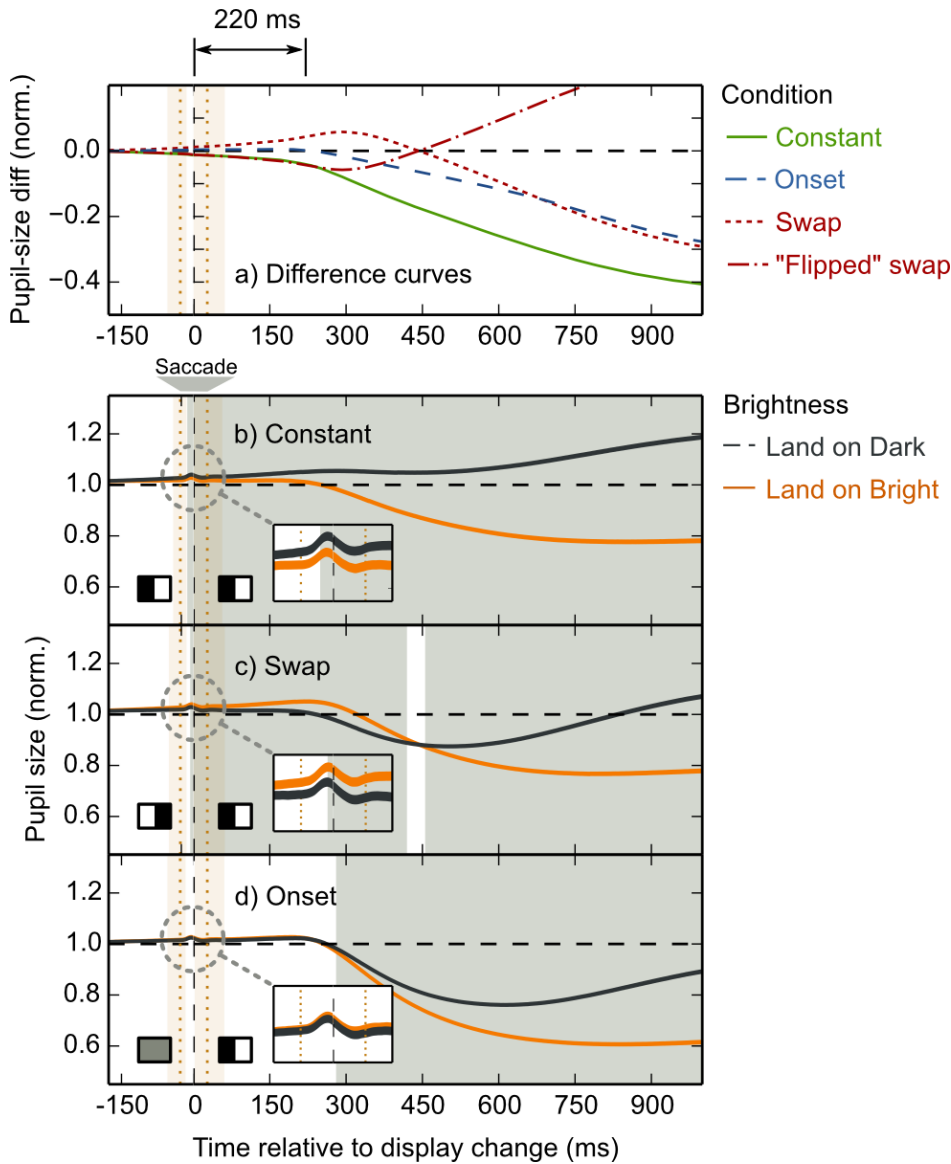
Figure 2. *a) Mean difference in pupil size between Land-on-Bright and Land-on-Dark trials for the three conditions as a function of time relative to display change. The PLR is shown as a negativity. The dot-dashed line shows the 'flipped' Swap condition, and is shown for comparison with the Constant 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 mean ± standard error. Background shadings indicate significant divergence between Land-on-Dark and Land-on-Bright trials (t > 2 for at least 200 consecutive samples). Inset panels zoom in on the -50 to +50 ms interval. Inset example displays schematically illustrate trial progression.*

*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 the earliest effects of luminance on pupil size, we conducted linear mixed-effects (LME) analyses with Participant as random effect on the intercept, 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. We considered divergence between Land-on-Dark and Land-on-Bright trials to be significant when $t > 2$ (cf. Baayen, Davidson, & Bates, 2008) for at least 200 consecutive samples (cf. Mathôt et al., 2013).

The effect of eye-movement preparation on the PLR was evident in two main ways. Firstly, in the Constant condition, divergence occurred already during the saccade, before the eyes had landed (from -9 ms until trial end; values relative to display change at time 0; see small inset panel in Figure 2b). This extremely rapid modulation of pupil size clearly shows that a PLR was prepared before saccade onset. As expected, divergence was observed much later in the Onset condition (+283 ms until trial end), in which preparation was not possible.

Secondly, in the Swap condition there was initially a (seemingly) inverse PLR, again arising during the saccade (-3 ms until +417 ms; see small inset panel in Figure 2c). Strikingly, the (flipped) Swap condition was qualitatively indistinguishable from the Constant condition until about 250 ms after the saccade (compare the dot-dashed and solid lines in Figure 2a). This suggests that it takes about 250 ms for the pupil to respond to the post-saccadic luminance, consistent with previous estimates of the PLR latency (e.g., Ellis, 1981; C. Wang & Munoz, 2014). From about 600 ms onwards the Swap condition was qualitatively indistinguishable from the Onset condition (compare the dashed and dotted lines in Figure 2a), suggesting that by this time the preparatory component of the PLR had fully dissipated.
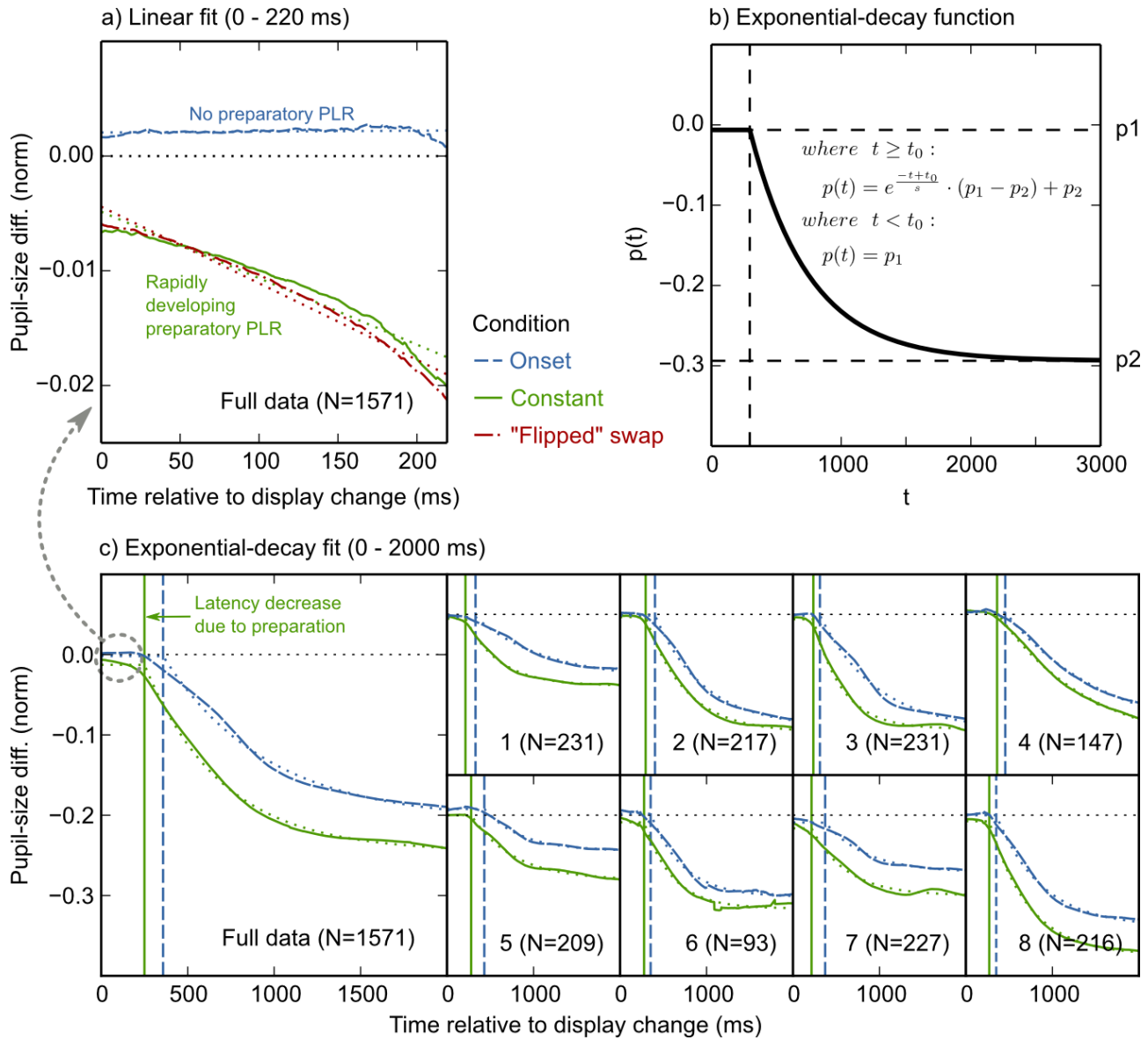
Finally, there was a slight pupillary dilation during the saccade, which is clearly visible in

the inset panels of Figure 2b,c,d. The origin of this intra-saccadic dilation is not clear. One possibility is that the physical forces that operate on the eye during a saccade cause a slight distortion of the iris' shape, which could be (artifactually) recorded as a dilation by the eye tracker (for a related technical point, see Nyström, Hooge, & Holmqvist, 2013). We note this effect for completeness only, as it is not specific to our experiment.

Modeling the PLR

A visual inspection of Figure 2a suggests that preparation qualitatively alters the shape of the PLR, rather than merely reduces its latency. More specifically, in the Constant condition, the PLR appeared to consist of a small, but rapidly developing bias that emerged already before the eyes landed (see the inset panel in Figure 2b). This initial bias was followed by a much more pronounced response, which we will call the 'full PLR'. We created two models to investigate whether the effect of preparation is limited to this initial bias, or whether the latency of the full PLR is reduced as well.

First, we modeled only the 0 - 220 ms interval, which we had defined as reflecting purely preparatory activity (Figure 3a). For each participant separately, we fitted a linear function to the mean difference response in the three conditions. To allow for direct comparison with the Constant condition, we 'flipped' the Swap condition. Next, we used paired-samples *t* tests to test for differences in slope and intercept, using a Bonferroni-corrected alpha level of .0083 (= .05 / 6 comparisons). This showed that the slope was lower (i.e. more negative) in the Constant ($t(7) = 5.19$, $p = .0013$) and Swap ($t(7) = 3.87$, $p = .0061$) conditions than in the Onset condition, whereas there was no significant difference between the Constant and Swap conditions ($t(7) = 1.23$, $p = .2581$). The comparisons for the intercept showed the same qualitative pattern, but were less reliable (Constant vs Onset: $t(7) = 2.69$, $p = .0310$; Swap vs Onset: $t(7) = 1.66$, $p = .1396$; Constant vs Swap: $t(7) = 0.34$, $p = .7460$). In sum, a linear model of the 0 - 220 ms interval revealed a rapidly developing PLR if, and only if, preparation was possible.

a) Linear fit (0 - 220 ms)

b) Exponential-decay function

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

c) Exponential-decay fit (0 - 2000 ms)

Figure 3. a) The difference in pupil size between Land-on-Bright and Land-on-Dark trials over time in the 0 -
220 ms interval. Solid, dashed, and dashed-dotted lines indicate observed grand mean responses. Dotted lines
indicate linear-model fits. b) The exponential-decay function used to model pupil-size difference (p(t)) as a
function of time since display change (t) during the 0 - 2000 ms interval. 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). c) Observed difference in pupil size between Land-on-Bright and Land-on-
Dark trials and model fits (dotted lines) for the Constant and Onset conditions (solid and dashed lines,
respectively). Vertical lines indicate full PLR latencies (t0) for the Constant (solid) and Onset (dashed)
conditions. The left pane depicts the grand mean response. The eight rightward panes show the mean responses
for each of the eight participants.

Next, we modeled a longer interval (0 - 2000 ms). We acknowledge that not all effects observed during this interval necessarily reflect preparatory activity, but we nevertheless feel that modeling a longer interval is informative. We chose an exponential-decay function, adapted from Hoeks & 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 3b). There are several other functions that fit the PLR about equally well, but the advantage of exponential decay 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`; a low `s` corresponds to a rapid decline). (The exponential-decay model assumes that pupil size is constant before `t0`. However, Figure 3a shows that preparation triggers slight pupil-size changes already before `t0`, although these are an order of a magnitude smaller than the 'full PLR' that arises later. It will be an important challenge for future research to improve models of the PLR to fully account for the effects of attention and eye-movement preparation.)

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 in a way that allows for direct comparison with the other conditions. Therefore, we modeled only the Constant and Onset conditions here. (See the Supplementary Materials for a model of the swap condition.)

We determined the model parameters for each participant, and tested for differences using a Bonferroni-corrected alpha level of .0125 (= .05 / 4 comparisons). Crucially, 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 than on Onset trials ($t(7) = 4.17$, $p = .0042$), as was final pupil-size difference ($t(7) = 3.56$, $p = .0093$). Response speed was slightly higher (i.e. a lower `s`, corresponding to a more rapidly declining function) in the Constant condition than in the Onset condition, but this difference was not reliable ($t(7) = 2.295$, $p = .0554$). In sum, the exponential-decay model confirms and extends the LME analyses by showing that preparation both induces

an initial bias (`p1`) and reduces the latency of the PLR (`t0`).

Accounting for gaze bias prior to saccade onset

When you attend to a stimulus without looking directly at it (i.e. covert attention), fixational eye movements tend to gravitate towards the attended stimulus (Engbert & Kliegl, 2003). Therefore, in our experiment, fixational eye movements could bring the eyes slightly closer to the (attended) saccade target already before the eyes set in motion. To control for this, we eliminated gaze bias through a pairwise-matching algorithm (cf. Mathôt et al., 2013). First, we determined the mean horizontal gaze deviation towards the cued side during the pre-saccade epoch for every trial. Next, we created pairs of trials with an opposite, but approximately equal bias (i.e. the summed bias was less than 0.03°). All trials that could not be paired were discarded (17.45%). This left a subset of trials in which there was no horizontal gaze bias (mean bias < .01°). The analyses described above were re-run on this subset of trials. This revealed virtually identical results to the full analysis (not shown; figures included in on-line supplementary analyses). However, it is worth mentioning that divergence in the Constant condition was observed even earlier in this analysis (from -105 ms until trial end). Crucially, this illustrates that our results are not due to a gaze-position bias prior to the eye movement, and demonstrates the robustness of the results.

Discussion

Here we report, for the first time, that the pupillary light response (PLR) is partly preparatory. 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., 2014, 2013; Naber et al., 2013).

When a PLR could be prepared before saccade onset, pupil size was affected by the luminance of a to-be-fixated surface even before the eyes had landed on it (Figure 2b). Given that

it takes 220 - 500 ms for the pupil to respond to luminance changes (Ellis, 1981; C. Wang & Munoz, 2014), this initial response must result from preparation. Strikingly, we could 'trick' the pupil into preparing for a luminance that was never brought into central vision, by changing the display brightness during the saccade (Figure 2c). This again suggests that the PLR has a preparatory component.

We created two models to obtain a qualitative picture of how the PLR is affected by preparation. First, we focused on the 0 - 220 ms interval, which we had defined as reflecting purely preparatory activity (Figure 3a). A linear model of this interval revealed that preparation triggered a weak, but rapidly developing PLR, which started already before the eyes had landed. Next, we created an exponential-decay model of the 0 - 2000 ms interval. This revealed that this rapid initial build-up was followed by a much more pronounced response, which we have called the 'full PLR' (Figure 3c). Because the full PLR occurs quite late, it is difficult to attribute differences in its latency unambiguously to eye-movement preparation. However, the fact that the full PLR occurred 100 ms earlier when preparation was possible, relative to when it was not, is again suggestive of preparation. Moreover, this latency reduction closely matches the finding that a covert shift of attention precedes every saccade by approximately 100 ms (Deubel, 2008; Rolfs & Carrasco, 2012). Therefore, we suggest that the preparatory PLR is driven by the pre-saccadic shift of attention.

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., 2014, 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 rivalry. In these studies, stimuli of different brightness are presented to each eye (e.g., Bárány & Halldén, 1948; Fahle, Stemmler, & Spang, 2011; Harms, 1937; Lowe & Ogle, 1966; Naber, Frassle, & Einhauser, 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 (Binda, Pereverzeva, & Murray, 2013b; Laeng & Endestad, 2012; Naber & Nakayama, 2013). Finally, and perhaps most strikingly, merely thinking about a bright stimulus induces a pupillary constriction (Laeng & 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.

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 (Deubel & Schneider, 1996; Kowler et al., 1995): The pupil prepares a light response as soon as attention shifts towards the target of an upcoming saccadic eye movement.

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