

Effects of attentional breadth and task difficulty on tonic pupil size

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Abstract

Changes in pupil size may accompany changes in perceptual needs. The present experiment investigated whether baseline pupil size is influenced by the breadth of attention, operationalized as the distance (i.e. eccentricity) from central vision at which attention is sustained. We designed a version of the attentional-breadth task (Brocher, Harbecke, Graf, Memmert, & Hüttermann, 2018) in which participants perform a visual memory task with stimuli appearing at different eccentricities. Crucially, we varied both target eccentricity and task effort independently. We expected tonic pupil size to linearly increase with the eccentricity at which participants sustain attention. This hypothesis was based on the idea that larger pupils may provide greater visual sensitivity, which would benefit the detection of stimuli appearing in peripheral vision. Furthermore, we expected tonic pupil size to increase as a function of the mental effort invested in the task, due to the hypothesized correlation between arousal and pupil size. Our results show that both target eccentricity and task difficulty had no effects on tonic pupil size, suggesting that these factors may have an effect only on the magnitude of transient pupil dynamics.

Introduction

To optimally perceive the environment, the sensory pathways of an organism need to be flexibly adjusted. Such optimizations can happen at different stages of sensory processing- from changes in individual neurons to precise movements such as eye-saccades, which require the coordination of vast amounts of information. In vision, the pupils play a key role in the very early stages of processing. They can optimize vision by allowing different amounts of photons to enter the eyes. Depending on their size, pupils may have different effects on visual perception. Small pupils let in a focused stream of light through the lens, thereby increasing the precision of the image projected on the retina (i.e. increasing acuity). Smaller pupils are also suited for clear vision across distances. Large pupils, on the other hand, let in more photons through the lens, decreasing the amount of light required to detect stimuli (i.e. increasing sensitivity), but producing a blurrier image on the retina. The biggest effect on pupil size, and a clear example of

how pupils optimize vision, is the Pupil Light Reflex (PLR) - the size of the pupils is changed based on environmental luminance.

There are two different timescales on which we could characterize changes in pupil size. Changes in tonic pupil size refer to changes in baseline pupil diameter over an extended period of time (e.g. a few seconds or more). Tonic pupil size is mostly determined by the luminance of the environment. It is not clear whether tonic pupil diameter is influenced by cognitive processing. It is likely that changes in tonic pupil size are accompanied by largely sub-conscious neural activity. In contrast to tonic pupil size, phasic changes describe pupil fluctuations that occur in a transient manner (e.g. pupil dilation quickly followed by re-constriction to baseline). Phasic responses often occur without any actual changes in luminance. These temporary fluctuations in diameter are usually evoked by factors such as arousal and cognitive load (Hess & Polt, 1960; Kahneman & Beatty, 1966), or orienting behaviors (Wang & Munoz, 2015). This broad category of evoked dilations can be categorized as psycho-sensory pupil responses, or PPRs. Generally, PPRs happen in response to events that require attention and action, and are usually triggered by the appearance of motivationally salient stimuli. In fact, a lot of pupil fluctuations are both structurally and functionally linked to attentional mechanisms for processing of the environment.

On a structural level, pupil size is largely mediated by evolutionarily old sub-cortical brain circuitry (Mathôt, 2018). Pupil constriction is driven by parasympathetic, whereas dilation – by sympathetic neural sites in the brainstem and spinal cord. The most often cited structure whose neural activity correlates with pupil diameter is the locus-coeruleus (LC), a nucleus in the brainstem thought to facilitate attention and behavior in various ways through its widespread neuromodulatory projections. The neurotransmitter supplied by the LC is norepinephrine (NE), which is believed to increase the firing rate of post-synaptic neural processing units. The adaptive-gain theory (Aston-Jones & Cohen, 2005) is a major theoretical framework describing the functioning of the LC-NE system. In general, it proposes that neural populations in the LC have two distinct modes of firing that both determine how NE is distributed throughout the central brain. Tonic mode relates to the overall level of activity of LC neurons, and its effects on task performance follow an inverted U shape. The adaptive-gain theory proposes that low levels

of tonic activity are associated with low levels of arousal, therefore drowsy and inattentive behavior; high levels of tonic activity are associated with active, easily distractible behavior. Medium levels of tonic activity are associated with best task performance. Medium levels also have the highest occurrence of phasic bursts, which are transient increases in the firing rates of some LC neurons. These phasic bursts are thought to follow the occurrence of motivationally salient stimuli, and to facilitate behavioral responses towards such targets. In summary, pupil size is hypothesized to correlate with activity in the LC. Tonic LC activity may underlie the overall arousal level of the central brain, whereas phasic bursts of LC activity may facilitate the processing of, and behaviors towards motivationally salient stimuli. Phasic pupil dilations are reportedly correlated with phasic bursts of LC activity (Richer & Beatty, 1987; Aston-Jones & Cohen, 2005).

The apparent correlation between phasic pupil dilations and phasic LC responses is attractive, however, there is no causal evidence to support the claim that phasic LC activity underlies phasic pupil dilations. There has been some evidence that phasic pupil responses are mediated by structures other than the LC. The Superior Colliculus (SC), a multi-layered structure in the midbrain, responsible for the generation of both overt and covert attentional shifts, has recently also been linked to the pupil circuitry (Wang & Munoz, 2015). The SC receives early stage visual information, and input from the cortical fronto-parietal attentional network. The SC plays a crucial role in the orienting response, which involves a series of goal-driven behaviors such as overt and covert shifts of attention towards novel, salient sensory information. Although the SC has connections to fronto-parietal circuitry, it is also theoretically part of an independent system involved in spatial orienting (Krauzlis, Lovejoy, & Alexandre, 2013). The transient pupil dilation mediated by the SC likely coevolved with the production of overt orienting responses, and we cannot exclude the possibility that such dilations may have a link with phasic LC activity. The Frontal Eye Fields (FEF) in the neo-cortex, another crucial processing site for overt and covert shifts of attention, have also been linked to the pupil circuitry. When electrically stimulated beyond a critical threshold of activation, neurons in the FEF initiate eye-saccades towards their receptive fields, and with sub-threshold stimulation they produce covert shifts of attention. Ebitz and Moore (2017) show that the amplitude of the PLR is modulated depending on whether a bright or dark stimulus appears in the receptive field of FEF.

neurons that receive sub-threshold electrical stimulation. In summary, the pupil circuitry can structurally be extended to areas of the brain that regulate overt and covert attentional control.

The findings of Ebitz and Moore (2017) suggest that pupil size is optimized based on the physical qualities of objects in the focus of attention. As a functional example of the relation between attention and pupil size, the PLR has been shown to be mediated by the luminance of covertly attended regions of visual space, even when controlling for luminance constancy and eye movements. A series of experiments shows that a small PLR can be observed when participants shift covert attention towards either bright or dark stimuli (Mathôt, van der Linden, Grainger, & Vitu, 2013); process words that convey a meaning of brightness or darkness (Mathôt, Grainger, & Strijkers, 2017), or even when mentally imagining bright or dark environmental scenes (Laeng & Sulutvedt, 2014). In summary, pupil size may be optimized based on the most active contents of perception, which are dependent on the focus of attention.

The contents of attention may have different perceptual qualities depending on where in the visual field they appear. For example, stimuli in peripheral vision suffer from reduced detectability and discriminability. Therefore, the perceptual quality of stimuli is reduced as they appear further into peripheral vision. It could be speculated that the act of covertly attending to stimuli in peripheral vision would benefit from large pupils, as they let more light in through the periphery of the lens. This would improve the detectability of such stimuli. A study by Mathot and Ivanov (in prep.) shows some evidence that larger baseline pupil size is associated with better performance on a simple visual detection task with stimuli appearing in peripheral vision. Given that the pupil circuitry is linked to various attentional control systems, is pupil size optimized based on the ‘breadth’ of attention? We define attentional breadth as the distance at which covert spatial attention is allocated, relative to where eye-gaze is fixated. In other words, attentional breadth refers to how far into peripheral vision the attentional ‘spotlight’ is extended. If having larger pupil size increases the detection rates for peripherally presented stimuli, does a larger attentional breadth dilate the pupils?

A study by Daniels et al. (2012) investigated the effect of attentional breadth on pupil size. The researchers presented participants with two sets of squares around a central fixation

point. The two sets were located at different eccentricities (i.e. visual angles), and visual cues instructed participants to shift their attention between the two sets. These cues involved rhythmical luminance changes of the displayed stimuli, for example, the disappearance of a set of stimuli, reductions in stimulus luminance, or switching the color of the fixation dot from white (for narrow attention) to black (for broad attention). The cues were rhythmically alternated at 0.2 Hz, which allowed the researchers to assess whether pupil fluctuations occur at this frequency via an FFT of the pupil time series. As the authors do not mention whether the cues were counterbalanced (e.g. whether a white fixation dot was also used to cue broad attention), we assume that such visual manipulations can induce changes in pupil size not attributable to covert attention. However, conditions in which participants shifted attention elicited significantly larger amplitude pupil fluctuations at 0.2 Hz than conditions in which the same display was observed passively. Thus, there is a reason to believe that the pupil fluctuations seen in Daniels et al. (2012) are partly due to the initiation of covert shifts of attention.

In a more recent study, Brocher et al. (2018) tested whether evoked pupil dilations scale with the eccentricity of targets in a visual memory task. On a trial-to-trial basis, participants in their experiments were cued to shift their attention covertly at different eccentricities, and memorize elements of visual stimuli presented there. Brocher et al. found that the amplitude of transient pupil dilations following stimulus onset was positively correlated with the eccentricity of the targets. The authors concluded that this reflects increased levels of mental effort required for larger (i.e. broader) shifts of covert attention. There are several methodological limitations in Brocher et al.'s study, which do not allow us to attribute this effect to covert attention. For example, only the target stimuli were shown each trial, which means that eccentricity conditions highly differed in terms of the visual content present on the display. It is likely that light coming from targets appearing far into periphery is simply lower than light coming from central stimuli, leading to pupil dilation. Furthermore, Brocher et al. did not account for the varying levels of mental effort exertion required when performing the task at different eccentricities. Conditions of higher eccentricity were associated with worse task performance. Therefore, the increased pupil dilation found by Brocher et al. might signal increased levels of cognitive load. Thus, it is not easy to conclude that the pupil effect observed by Brocher et al. is due to attentional shifts alone.

We borrow aspects of Brocher et al.'s attentional-breadth task, hoping to address some of the methodological limitations in their original study. We will attempt to control for both visual differences between experimental conditions, and differences in effort when performing the task at larger eccentricities. Therefore, we designed an experimental task in which we vary both stimulus eccentricity and task difficulty independently of each other. We believe these controls are important to assess whether the proposed attentional breadth pupil effect can be dissociated from an effect of mental effort. We will diverge from the analysis of the original study in one significant way – we will investigate baseline rather than transient pupil diameter. Because we wish to vary both eccentricity and difficulty independently, we opted for a blocked experimental design. This means that baseline pupil diameter will be different between the levels of our factors. Thus, we will be able to assess only differences in baseline pupil size, and not transient responses, as there is no common baseline to correct for.

There is some evidence that sustained spatial attention does not affect baseline pupil size. In one of the experiments in Daniels et al. (2012), participants switched attention between stimuli at two eccentricities on a trial-to-trial basis, which had no effect on baseline pupil size. We will investigate whether sustaining attention at an eccentricity over the course of 56 trials, much longer than in Daniels et al.'s study, can elicit an effect on baseline pupil size. With regards to the effects of mental effort on baseline pupil size, under the assumptions of the adaptive-gain theory the LC should be in different levels of tonic activity between blocks that significantly differ in difficulty, as this requires investment of different levels of mental effort into the task. If LC activity is as tightly coupled with pupil diameter as the literature suggests, under the adaptive-gain theory we expect that blocks of increased task difficulty will elicit larger tonic pupil diameter.

Hypotheses

Our main hypothesis is that baseline pupil size will positively correlate with the eccentricity at which participants sustain their attention. Put differently, experimental blocks in which target stimuli appear at larger eccentricities will be associated with increased tonic pupil

diameter, compared to blocks with more central stimuli. Such an effect would be dissociable from effects of arousal by controlling for task difficulty across eccentricities.

Another aim of this thesis is to assess whether baseline pupil diameter increases in response to periods of sustained mental effort or arousal, both functional concepts related to the LC-NE system. Our secondary hypothesis is that baseline pupil size will negatively correlate with behavioral performance. In other words, tonic pupil diameter will be larger the more errors participants make in an experimental block. We assume that lower accuracy is analogous to increased levels of mental effort.

Methods and Procedure

Participants

26 participants performed our experiment and received course credits in return. We recruited participants using the University of Groningen's first-year Psychology participant pool, with the requirement of normal vision without glasses or lenses. The experiment plan was approved by the Ethical Committee Psychology (ECP).

Materials and Design

We used OpenSesame version 3.2.1 (Mathôt, Schreij, & Theeuwes, 2012) with the PsychoPy backend (Peirce, 2007) for the generation of our experiment. Experimental stimuli were presented on a 27-inch iiYama ProLite E2773HS monitor, at 1920 x 1080 px resolution and 60 Hz refresh rate. A white fixation dot (10x10 px, 0.25°, lum: 103,53 L) was constantly presented in the center of a gray (lum: 58,723 L) display. Three gabor patches were constantly presented on the horizontal axis of the display, on both sides of the fixation dot (six gabors in total), at eccentricities of 3.3 ° ('near'), 7.2 ° ('mid'), and 13 ° ('far'). The luminance of all gabors ranged from 45.62 to 71.42 L. The scale of the gabor patches increased linearly depending on their eccentricity – stimuli nearest to the fixation dot were 60x60 px (1.3°), stimuli at the middle eccentricity were 70x70 px (1.8°), and stimuli at the furthest eccentricity were 120x120 px (2.5°).

This manipulation of size, reminiscent of cortical magnification scaling, was done in order to compensate for the reduced visibility of stimuli in peripheral vision. The parameters for this scaling were the same for all participants. The spatial frequency of the gabor patches also increased with their eccentricity: ‘near’ – 0.025; ‘mid’ – 0.027; ‘far’ - 0.03. This means that the number of oscillations within the gabor patches slightly increased with their eccentricity.

In order to further minimize differences in mental effort between eccentricity blocks, we implemented a staircase procedure per level of eccentricity (i.e. three independent staircase procedures). The staircase procedure is used for keeping task accuracy around a certain set-point. This algorithm tracks the proportion of correct and incorrect responses on a trial-by-trial basis, and adjusts the orientation of target stimuli to be either further or closer away from their vertical axes in a range from 1 ° to 45 °. We assume this manipulation influences the discriminability of target orientations, making the task easier or harder to perform.

Procedure

At the beginning of each session, participants were asked to remove eye make-up if necessary. After reading through the instructions for the experiment, they were asked to sign an informed consent sheet. Participants’ head movements were limited by using a chin-and-forehead rest. An EyeLink 1000 (SR Research, Mississauga, ON, Canada) video based eye-tracking camera was used to obtain both eye-movement and pupil size data (area) from each participant’s right eye, at a sampling frequency of 1000 Hz. The EyeLink’s threshold for pupil detection was set to automatic, and manual adjustments were made depending on whether erroneous detections occurred outside of the pupil. After setting the pupil detection threshold, a four-point eye-gaze calibration was performed.

Participants had to perform a task (Figure 1) similar to the attentional-breadth task in Brocher et al. (2018). We varied both target eccentricity, and the task’s overall difficulty independently of each other, in a blocked manner. The order of the two levels of factor ‘difficulty’ (‘easy’, ‘hard’) was fully counterbalanced across participants. For each participant, a single permutation of the three levels of factor ‘eccentricity’ (‘near’, ‘mid’, ‘far’) was generated,

and repeated for both the practice blocks and the two ‘difficulty’ conditions. Each participant first performed three practice blocks of 48 trials in each eccentricity, followed by six experimental blocks of 56 trials. Three experimental blocks had the ‘easy’, and three blocks – ‘hard’ difficulty, both tested at every eccentricity.

Each block started with a written instruction letting the participant know at which eccentricity the targets will be appearing throughout the block. Participants had to maintain eye fixation in the center of the screen. Before each trial, a drift-correction procedure was initiated. At the start of each trial, all gabor patches were oriented horizontally (0°). After a period of 2000 ms. (‘baseline phase’), all gabor patches changed their orientation for 250 ms. (‘target phase’). During each block, the same two bilateral gabor patches were targets, characterized by a slight tilt in orientation to the left or right of their vertical axes. Distractor stimuli changed to 90° vertical orientation. Both targets had the same degree of orientation, only their direction could vary. Following the target phase, all stimuli reverted back to their initial horizontal orientation and participants had to retain target orientations in memory for 750 ms. After that, two white bars consecutively appeared under the locations of the targets, cueing participants to indicate the direction of each target’s orientation (by pressing the ‘left’ or ‘right’ arrow keys). Responses were not timed. A correct response was recorded only when both target directions were reported correctly. Within each experimental block, all possible combinations of target directions and response cue sequences were generated, and their order of appearance was randomized (without replacement).

Over the course of each block, three independent staircase procedures (one for each eccentricity) controlled the proportion of correct responses within a certain set-point. For the three practice blocks, the accuracy set-point of each staircase procedure was set to an intermediate value of 75%, and the starting degree of orientation of targets was 45° . At the end of each practice block, the last degree of orientation generated by the staircase procedure was used for starting values for each respective eccentricity block in the rest of the experiment. Experimental blocks had set-points of either 90% (‘easy’) or 60% (‘hard’). This manipulation constitutes our second independent variable – task difficulty.

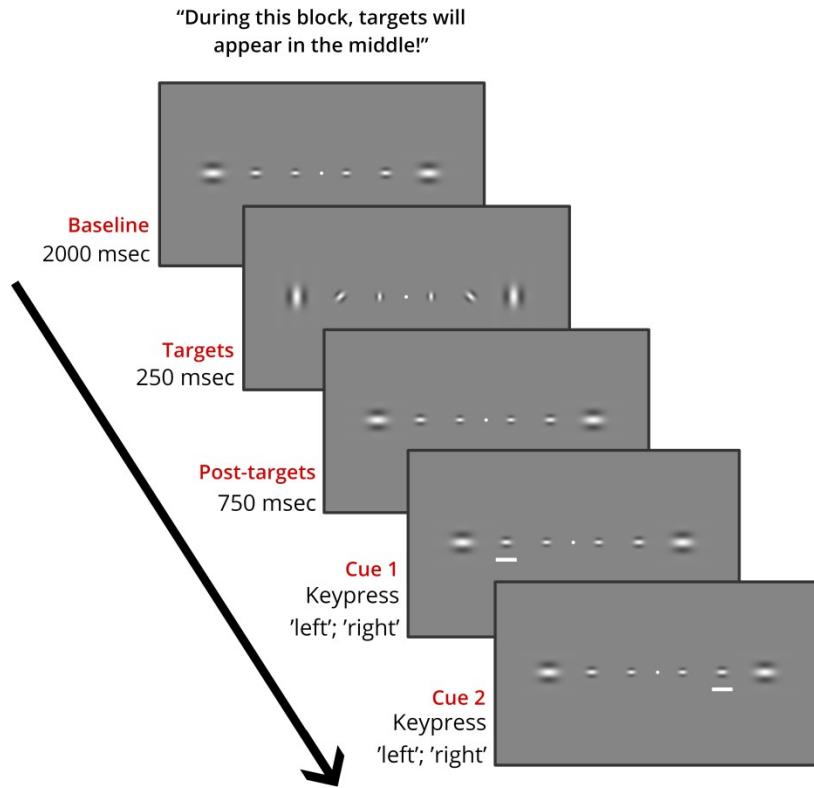


Figure 1 - Schematic depiction of a trial (see ‘Methods and Procedure’ section for details). This is an example of a block in which only stimuli in the middle eccentricity are tested. Stimuli are not drawn to scale.

Results

The experiment had a 3x2 repeated measures design with categorical factors: ‘eccentricity’ (levels: ‘near’, ‘mid’, ‘far’); and ‘task difficulty’ (levels: ‘easy’, ‘hard’). All statistical analyses were performed only with data from experimental blocks.

Behavioral analysis

A custom R script was used for behavioral analyses (R Core Team, 2016). Accuracy was defined as the proportion of correct answers within a block. Differences in accuracy between blocks were assessed with a two-way Bayesian repeated-measures ANOVA (R formula:

‘accuracy’ ~ ‘eccentricity’ x ‘difficulty’ + ‘subject’) with ‘subject’ as random factor (BayesFactor, 2016). The prior probability distribution was set at 0.5. This analysis gives us strong (Jeffreys, 1961) evidence against a main effect of eccentricity ($BF_{10} = 0.075$), and moderate evidence towards a main effect of difficulty ($BF_{10} = 5.113$). These results go in line with an NHST version of the same analysis (‘eccentricity’: $F(2) = 0.803, p = 0.450$; ‘difficulty’: $F(1) = 597.355, p < 0.01$). These results suggest that our difficulty manipulation succeeded in controlling accuracy levels between eccentricities, and successfully made the task more challenging between difficulty levels.

Pupil analysis

Analysis of pupil data was done with a custom Python script (Python 3). Segments of data that contained blinks were reconstructed using cubic-spline interpolation. All pupil data was down-sampled from 1000 to 100 Hz. A window of the first 200 samples (i.e. first 2000 ms.) of each trial was subset and used for the following statistical analyses.

Differences in baseline pupil size between ‘eccentricity’ and ‘difficulty’ levels were assessed with linear mixed effects models using the lme4 R package (Bates, Maechler, Bolker, & Walker, 2015) over each sample of the pre-processed pupil time series (Figure 2). The levels of categorical variables were recoded as -1,1 for ‘difficulty’, and -1,0,1 for ‘eccentricity’. The models include only main effects for eccentricity and difficulty, a random factor for subject, and random slope and intercept per subject (R-formula: ‘pupil size’ ~ ‘eccentricity’ + ‘difficulty’ + (1 + ‘eccentricity’ + ‘difficulty’ | ‘subject’)). Alpha was kept at 0.05 for all comparisons. The final model indicates that there were no significant main effects of either ‘eccentricity’, or ‘difficulty’ at neither time point in the series (‘eccentricity’: $\min t(25) = -2.041, \min p = 0.052$); ‘difficulty’: $\min t(25) = -0.152, \min p = 0.709$). Tonic pupil diameter did not significantly differ between the three levels of eccentricity and two levels of difficulty. Therefore, we did not run a model including interaction effects. The model estimates for a linear effect of ‘eccentricity’ show a weak negative effect, ranging from – 28.14 to – 19.29. The estimates for ‘difficulty’ ranged from -2.48 to 6.92. Given the high variability within and between subject pupil diameters, we can assume these estimates to be the result of random error.

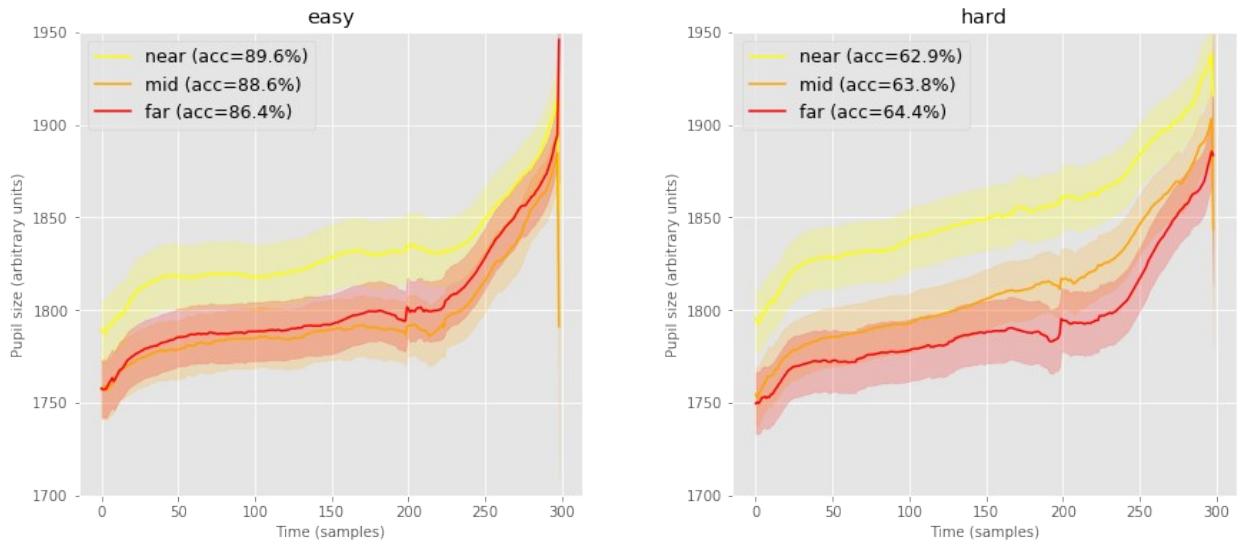


Figure 2 - Average-trace plots, split between the two levels of difficulty. Each separate trace represents averaged pupil size within each eccentricity condition.

As a further analysis, we inspected the linear relationship between mean pupil size and eccentricity, separately for each subject. We did this in order to assess whether the apparent weak negative relationship between pupil size and eccentricity is reliable across participants. We split the dataset by subject number and difficulty levels, and carried out a linear regression with mean pupil size as dependent variable, and eccentricity as independent variable. The slope estimates of these models (Figure 3) suggest that the relationship between mean pupil size and eccentricity for many subjects was negative. There were more negative slopes in the ‘hard’ difficulty. A negative slope would indeed indicate a result in the opposite direction of our main hypothesis, however only 2 out of 52 model estimations were statistically significant.



Figure 3 - Rank-ordered slopes describing the linear relationship between mean pupil size and eccentricity, for each individual participant. Each dot represents the slope's value, and error bars represent standard error.

Discussion

Based on previous findings (Brocher et al., 2018; Daniels, Nichols, Seifert, & Hock, 2012) we expected baseline pupil size to scale with the eccentricity at which participants sustain covert attention. Our experimental task was an adapted version of the attentional-breadth task of Brocher et al. (2018). We varied both target eccentricity and task difficulty independently of each other. Differences in accuracy between eccentricities were successfully limited by the use of staircase procedures controlling the difficulty of the task. The staircase procedures also allowed us to create separate conditions for task difficulty. We expected baseline pupil diameter to increase as a function of task difficulty.

Sustaining attention at different eccentricities does not affect baseline pupil size. Contrary to our expectations, the relationship between pupil diameter and eccentricity was negative for many subjects. However, there was a large degree of error within each subject's data. Therefore, if differences in pupil size between eccentricities exist, our statistical power would not be sufficient to detect them. Even if pupil dilation scales with the eccentricity of attended stimuli,

this kind of response is likely transient in nature, and occurs as part of an orienting response. The orienting response occurs at a timescale far smaller than the pupil data we analyzed, and is driven by exogenous attention and sudden visual onsets. In summary, our results provide some evidence that tonic pupil size does not change as a function of the breadth of attention.

Our results also suggest that baseline pupil diameter does not correlate with different levels of sustained mental effort. In contrast with our blocked experimental design, studies that have investigated the relation between effort and pupil diameter have focused mostly on transient responses, or trial-to-trial comparisons of baseline pupil diameter (e.g. Daniels, Nichols, Seifert, & Hock, 2012; Unsworth & Robison, 2017). Our results support the general pattern of results in the literature: moment-to-moment differences in mental effort and cognitive load affect pupil diameter in a transient manner, whereas sustained levels of effort do not affect tonic pupil diameter. We can interpret our results in two ways. First, if the level of LC-NE tonic activity is indeed correlated with different levels of mental effort, our results suggest that tonic pupil diameter is not correlated with tonic LC-NE activity. If a correlation between tonic LC-NE activity and tonic pupil size truly exists, our results indirectly suggest that the LC-NE system is not in heightened levels of tonic activity during long periods of effortful processing.

Differences in task-evoked pupil responses could not be compared, which is a big limitation to our experimental design. Differences between the amplitudes of the transient responses in our task would most likely indicate that stimuli at some eccentricities were more difficult to hold in memory. However, both the design of the stimuli and the implementation of staircase procedures should be able to negate possible differences in effort. Finding differences in the amplitude of evoked dilations would therefore suggest an attentional breadth component to transient pupil dynamics.

Given the large amount of variability in our sample, we can reasonably conclude that all evidence goes against both effects of target eccentricity and task difficulty on tonic pupil size. Further experiments could benefit from a design that limits between-subject variability, and allows for more precise model estimates within each subject - for example, testing a smaller number of subjects over a larger number of repetitions per condition.

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