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Effects of pupillary responses to luminance and attention on visual spatial discrimination

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The optic quality of the eyes is, at least in part, determined by pupil size. Large pupils let more light enter the eyes, but degrade the point spread function, and thus the spatial resolution that can be achieved (Campbell & Gregory, 1960). In natural conditions, the pupil is mainly driven by the luminance (and possibly the color and contrast) at the gazed location, but is also modulated by attention and cognitive factors. Whether changes in eyes' optics related to pupil size modulation by luminance and attention impacts visual processing was assessed in two experiments. In Experiment 1, we measured pupil size using a constantly visible display made of four disks with different luminance levels, with no other task than fixating the disks in succession. The results confirmed that pupil size depends on the luminance of the gazed stimulus. Experiment 2, using similar settings as Experiment 1, used a two-interval forced-choice design to test whether discriminating high spatial frequencies that requires covert attention to parafoveal stimuli is better during the fixation of bright disks that entails a small pupil size, and hence better eyes' optics, as compared to fixating dark disks that entails a large pupil size, and hence poorer eyes' optics. As in Experiment 1, we observed large modulations of pupil size depending on the luminance of the gazed stimulus, but pupil dynamics was more variable, with marked pupil dilation during stimulus encoding, presumably because the demanding spatial frequency discrimination task engaged attention. However, discrimination performance and mean pupil size were not correlated. Despite this lack of correlation, the slopes of pupil dilation during stimulus encoding were correlated to performance, while the slopes of pupil dilation during decision-making were not. We discuss these results regarding the possible functional roles of pupil size modulations.

Introduction

Pupil activity is controlled by antagonistic highly dissimilar pathways associated with adrenergic and cholinergic neuromodulation: the parasympathetic pathway drives luminance-based pupil constriction through a short circuit involving retinal ganglion cells (RGCs) and intrinsically-photoreceptive retinal ganglion cells (ipRGCs), the pretectal nucleus, the Edinger-Westphal nucleus, and the ciliary ganglions that innervate the iris sphincter; in contrast, the sympathetic pathway driving pupil dilation involves the frontal cortex, the hypothalamus (that sends inhibitory inputs to the Edinger-Westphal nucleus), and the locus coeruleus whose activity correlates with pupil dynamics (Aston-Jones & Cohen, 2005); the ophthalmic branch of the sympathetic nerve then runs down to C8-T2 in the spinal cord, reaches the superior ciliary ganglions whose output nerve runs along the carotid vein before innervating the iris dilator muscles (Szabadi & Bradshaw, 1996). This very peculiar pathway involves subcortical and cortical structures related to the modulation of internal cognitive states, in line with the numerous studies showing that pupil dilation is under the control of a number of cognitive factors such as perception, attention, memory load, cognitive load, expectation, prediction, decision, etc. (Kahneman, Beatty, & Pollack, 1967; Bouma & Baghuis, 1971; Beatty & Wagoner, 1978; Beatty, 1982; Partala, Jokiniemi, & Surakka, 2003; Partala & Surakka, 2003; Merritt, Schnyders, Patel, Basner, & O'Neill, 2004; Privitera, Renninger, Carney, Klein, & Aguilar, 2008; Hupé, Lamirel, & Lorenceau, 2009; Einhauser, Koch, & Carter, 2010; Preuschoff, Hart, & Einhauser, 2011; Mathôt, Van der Linden, Grainger, & Vitu, 2013;

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Binda & Gamlin, 2017; de Gee, Knapen, & Donner, 2014; Zekveld, Heslenfeld, Johnsrude, Versfeld, & Kramer, 2014).

Thus, at any time, the size of the pupil reflects the balance between parasympathetic and sympathetic inputs, although to different degrees and with different dynamics: cognitive-based pupil dilation is generally slower and of modest amplitude as compared to luminance-based pupil constriction. In most studies, these antagonistic inputs to the pupil are studied independently: studies concerned with the influence of low-level stimulus characteristics (e.g., clinical studies) generally assume that cognitive factors do not significantly influence pupil measures, while studies aiming at identifying the influence of high-level cognitive factors attempt to use stimuli whose low-level characteristics are stable and mostly unchanging during the course of a trial, to avoid possible confounds due to changes in stimulus parameters that could account for, or mask, changes in pupil size.

Importantly, pupil responses to light depend upon the retinal location of the inducing stimuli, with ample pupil modulations elicited by stimuli presented in central vision, while peripheral stimuli elicit smaller pupil responses, whose amplitude are heterogeneous in the visual field (Hong, Narkiewicz, & Kardon, 2001; Clarke, Zhang, & Gamlin, 2003). This retinal heterogeneity of the pupil response to light should not, in principle, occur with cognitive-based pupil modulations—with the exception of focused spatial attention (Binda, Pereverzeva, & Murray, 2014; Rosli et al., 2018)—that involve the sympathetic pathway.

Whatever the origins of pupil size modulation, changing pupil size modifies the eyes' optics (spherical aberrations, point spread function), which in turn impacts visual acuity and spatial frequency processing (Shlaer, 1937; Baker, 1949; Campbell & Gregory, 1960; Campbell & Gubisch, 1966; Robson, 1966; Bradley & Skottun, 1987; Carkeet, Leo, Khoo, & Au Fong, 2003). It must, however, be stressed that in the seminal work of Campbell and Gregory (1960) demonstrating that pupil size impacts visual acuity and contrast sensitivity, the pupil was dilated and paralyzed with drugs, and subjects saw the stimuli through artificial pupils of fixed diameter that were parametrically varied. Thus, psychophysical measurements demonstrating the influence of pupil size on perception were performed in these very peculiar conditions. It is not obvious that these findings would hold in everyday life, as pupil size constantly varies, either because of its intrinsic properties (pupil constriction is followed by a pupil escape), or due to—explicit or implicit—visual and cognitive tasks that accompany, and drive, visual exploration. Although it is often argued that large pupils let more light enter the eyes, the benefit of this increased amount of light should mostly be useful in scotopic, low light condi-

tions. In photopic conditions, the advantage of letting more light enter the eyes is less obvious, and it seems paradoxical that cognitive factors, such as visual attention, dilate the pupil in photopic conditions, which entails a poorer optic quality of the retinal image, and could thus impair visual processing.

These different observations motivated the present study whose aims were (a) to measure pupil size as a function of the luminance of foveally fixated targets to provide baseline results; (b) to test whether spatial frequency discrimination performed with high spatial frequency Gabor patches, that requires covert attention to parafoveal stimuli, differed as a function of pupil size, when the latter is constrained by the luminance level of a gazed target.

Experiment 1: Pupil dynamics during fixation of targets with different luminance

The goal of this experiment was to characterize the dynamics of pupil responses evoked by successive fixations of disks of different luminance simultaneously and continuously present on a stimulation screen during a trial. This setting resembles what is encountered in ecological conditions where individuals make successive saccades to targets with different luminance with otherwise constant illumination, and serve to establish a baseline pupil activity in the absence of a perceptual task. In line with previous results, we expected that pupil size would vary with the luminance level of the foveated target.

Participants

Fourteen healthy participants (seven females and seven males) aged 20 to 27 years old (F: 23.7 ± 1.9 years old, M: 24.8 ± 1.6 years old) were tested. Inclusion criteria were: no history of past or present ocular pathologies or general diseases that could affect pupil responses; no use of topical or systemic medications that could affect pupil responses; no known strabismus or eccentric fixation; visual acuity $\geq 10/10$ at the monitor distance (75 cm) corrected only with contact lenses; no senile miosis (subjects older than 40 years old were excluded). The absence of anisocoria and abnormality of direct, consensual pupillary reflexes and the relative afferent pupillary defect test (RAPD) were also verified for each subject to ensure no pathology affected pupil responses. All participants provided informed written consent. The protocol was conformed to the Declaration of Helsinki.

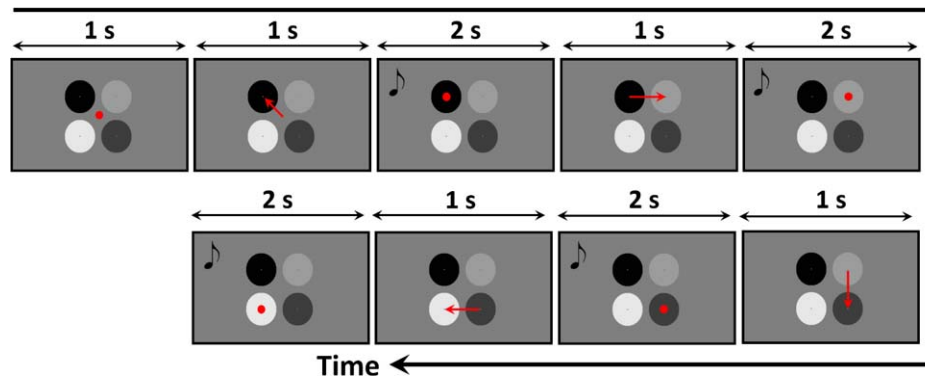


Figure 1. Design and time course of Experiment 1. For illustrative purposes, red dots indicate the location of eye fixations and red arrows represent the saccades made to move from one disk to another. The trial began with a central fixation point (a 0.6° circle, 60 cd/m^2), which disappeared after 1 s, indicating that the participants must fixate the first upper left disk. The sequence of fixations was paced by a saccade triggering beep. During a trial, four beeps of 2 s each corresponding to the fixation period were played, with silence of 1 s in between. When the sound stopped, participants had to make a saccade to the next fixation disk. The fixation sequence was always clockwise. A small gray dot at the center of each disk (0.04° , 95.5 cd/m^2) was provided to help maintaining fixation.

Apparatus

Eye movements and pupil size were recorded monocularly using an infrared video-based eye tracker (EyeLink II; SR Research, Ltd., Ottawa, Canada), sampled at 500 Hz. Visual stimuli were presented on a LCD monitor (ASUS, Taipei City, Taiwan; 37.98° wide, 21.58° high with a display resolution of $1,024 \times 768$ pixels and a refresh rate of 120 Hz, positioned 75 cm from participant's eyes). Experiments were conducted in darkness. To isolate the subject's visual field from the experiment room light, subjects were looking at the stimulation monitor through a black square tube placed between their head and the screen.

Stimulus and procedure

Pupil size was measured before the main experiment for each participant under photopic and mesopic conditions (mean pupil size \pm SD: mesopic conditions: 4.5 ± 0.5 mm; photopic conditions: 3 ± 0.2 mm). To characterize the dynamics of pupil responses as a function of the luminance of the gazed targets, we designed a stimulus consisting in four disks (4.4° diameter) with different luminance (1, 48, 143, and 191 cd/m^2) displayed on a gray background (95.5 cd/m^2). The disks were positioned at 3.7° from the monitor center and distributed in a square shape (Figure 1). The luminance levels were chosen so that the overall mean luminance was similar with and without the disks.

Participants were instructed to fixate each of four disks during 2 s in succession. A beep sound (pure tone, 400 Hz), was used to pace successive fixations. The beep was played during 2 s to indicate that participants must fixate a target, stopped during 1 s to trigger a

saccade to the next disk, and so on. These saccades are referred to as “positioning saccades” in the following (PS). The first target disk was always upper-left, the second top-right and so on. A trial started with 2 s of fixation of a dot at the monitor center, which then disappeared to inform participants to fixate the first disk. There were four disk configurations to avoid a systematic link between luminance and position: 1. black, light gray, dark gray, and white; 2. white, black, light gray, dark gray; 3. dark gray, white, black, light gray; 4. light gray, dark gray, white black. A 2 s interstimulus interval separated the trials, during which a uniform medium gray background (95.5 cd/m^2) was presented. Conditions were randomly chosen and repeated 18 times in three sessions of 24 trials (within the same day) for a total of 72 fixations of 2 s per luminance level.

Data analysis

The recorded eye movements and pupil data were analyzed offline using custom MATLAB (The Math-Works, Natick, MA) scripts. The pupil data set is available at: http://neuromorphic-vision.com/public/downloads/pupilData_Ajasse_Lorenceau/

Pupil dynamics, sampled and analyzed at the screen refresh rate (120 Hz), were processed as follows (see Figure 2):

1. Blinks were first detected and replaced by a linear extrapolation.
2. Pupil recordings were smoothed using a sliding average (83 ms time window, 10 samples).
3. Pupil size was then normalized relative to a baseline (average pupil size during 0.5 s of central fixation with the four disks visible).

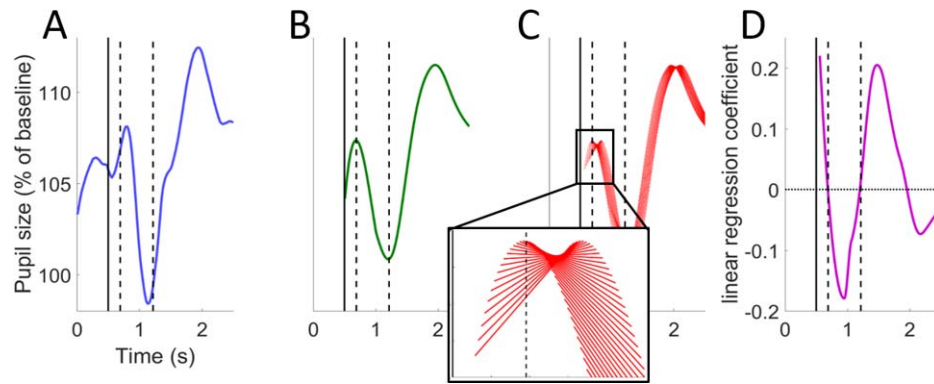


Figure 2. Data analysis. Each panel shows pupil size modulation (in percentage of base line) over time. In each plot, the solid vertical black line denotes the start of a fixation epoch corresponding to the end of the saccade triggered by the sound; vertical dashed black lines represent the inflection points computed on the pupil signal, corresponding to the constriction latency (left) and the latency of maximum constriction (right). (A) Raw pupil signal after cleaning and smoothing (blue); (B) low-pass filtered (1 Hz) pupil signal (green); (C) sliding linear regressions used to compute the inflection points (red); (D) linear regressions coefficients (purple). Positive values correspond to dilating pupil; negative values represent constricting pupil. The zero crossings correspond to inflection points, used to label the beginning and the end of a constriction.

4. Saccades were detected based on horizontal and vertical eye movements using a velocity threshold of $50^\circ/\text{s}$ and or an acceleration threshold of $1,500^\circ/\text{s}^2$, and an amplitude threshold of 2° . The criteria used to distinguish PS from spurious saccades were:
 - a. Saccade direction consistent with the course of the trial. In Experiment 1, four positioning saccades are performed: a first oblique upward and leftward saccade, a second horizontal-rightward saccade, a third vertical-downward saccade, and a fourth horizontal-leftward saccade.
 - b. Temporal occurrence of PS consistent with the course of the trial. In Experiment 1, the temporal window of interest ranges from 0.5 s before the end of the sound beep (in case of anticipated saccades) to 1.5 s after the sound end (0.5 s lag). If no saccade meeting these criteria was detected, the corresponding portion of the trial was excluded from further analysis.
5. To analyze the pupil dynamics following positioning saccades, a linear regression on a sliding time window of 108 ms was computed on low-pass filtered pupil signal (1 Hz). This allowed finding inflection points on the pupil signal, representing the beginning and the end of pupil constriction. If no inflection point was detected, or if the first inflection point (beginning of constriction) was detected after 1.5 s, or the second inflection point (end of constriction) was detected before 0.25 s after the end of a saccade, the trial was excluded from further analysis.

Using these strict criteria led to the exclusion of 8.79% of the trials in Experiment 1, and 16.07% of the trials in Experiment 2 (the distribution of rejected trials is shown in Supplementary Figure S2C, F).

1. The variables of interest computed on valid trials were:
 - a. The mean pupil size and pupil size variance computed for each fixation period (i.e., in-between two positioning saccades).
 - b. The latency of the start of a constriction: the time between the end of a positioning saccade to the first inflection point computed on pupil signal (see aforementioned and Figure 2).
 - c. The postsaccadic dilation amplitude: the difference of pupil size at saccade end and the beginning of constriction.
 - d. The constriction amplitude, computed as the difference of pupil size at the beginning and the end of a constriction, defined by the inflection points computed on the pupil signal.
 - e. The latency of the end of the pupil constriction: the time between the positioning saccade and the second inflection point.
 - f. The constriction velocity, defined in percentage of baseline per second: the constriction amplitude divided by the time between the first and the second inflection points of the pupil signal.
 - g. The quality of fixation: the percentage of the time during which the gaze position was inside a spatial window of 1° centered on the target disks.
2. To determine the effect of luminance on the variables defined already, linear regressions were processed for each participant on valid trial across conditions. The average and the 95%

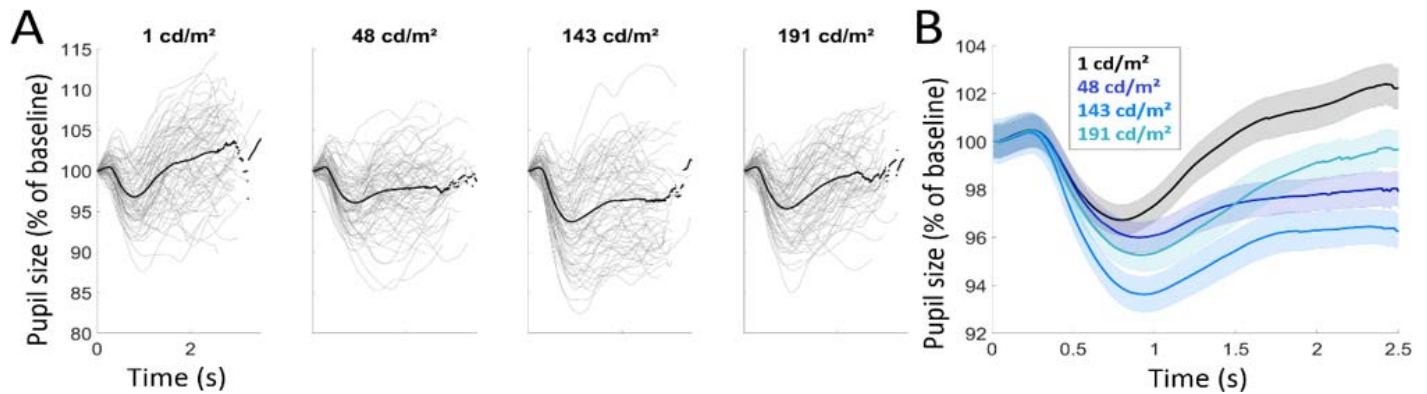


Figure 3. (A) Pupil size (in percentage of base line) over time of one participant, as a function of target luminance: individual trials (light gray lines) and average (thick black line) are shown. (B) Average pupil size over time and 95% CI for each target disk luminance.

confidence intervals of the regression slope coefficients were computed on the population of participants. In the following, we indicate the slope of the linear regression, denoted SLR, and the confidence interval, CI, for each of the analyzed variables.

Results

Before analyzing pupil dynamics in detail, we checked both the quality of fixation and the saccadic activity, to ensure that participants correctly performed the task (see Supplementary Figure S1). Saccadic activity was overall consistent with the constraints of the tasks (see examples in Supplementary Figure S1A) and fixation was overall stable (from 90% to 100% of the time spent within a 1° window), except for participant S09 (see Supplementary Figure S2A–B). Accordingly, we found no significant correlation between target luminance and fixation stability (SLR: $a = -2.86e-04$; CI = $9.40e-03$; Supplementary Figure S2A). In addition, comparing the pupil responses for the different spatial distribution of luminance levels revealed no significant effect. We therefore pooled the pupil data as a function of the luminance level, independently of their position in the visual field.

For all subjects, mean pupil size was computed on fixation periods, sorted by luminance level. Figure 3 presents pupil size as a function of the luminance of the fixated disk (single trials and mean) of one subject. The full data set of the 14 participants is presented in Supplementary Figure S3–S5.

As it can be seen in Figure 3, the pupil slightly dilated after a PS, then constricted to reach a minimum size after a delay, and dilated again while participants fixated a target disk (pupil escape). This pattern was observed for most participants and trials, although a

high variability across participants was observed (Figure 3 and Supplementary Figure S3–S5).

We then analyzed the different variables describing pupil dynamics (Figure 4). We found a significant effect of target luminance on the average pupil size (SLR: $a = -1.65e-2$; CI = $3.49e-3$; Figure 4A), with pupil size decreasing with increasing target luminance. The variance of pupil size also increased with target luminance with a low-to-medium effect size (average and CI in percentage of baseline: 1 cd/m^2 : 3.16 ± 0.51 , 48 cd/m^2 : 2.85 ± 0.58 ; 143 cd/m^2 : 3.55 ± 0.63 , 191 cd/m^2 : 3.54 ± 0.75 ; SLR: $a = 3.02e-3$; CI = $1.31e-3$; not shown).

Following a PS, we observed an initial dilation whose amplitude correlated with target luminance (SLR: $a = -3.94e-3$; CI = $1.51e-3$; Figure 4B), as did the postsaccadic pupil constriction (PSPC) amplitude (SLR: $a = 2.32e-2$; CI = $4.46e-3$), despite a plateau effect for the highest luminance contrast (Figure 4D). PSPC velocity also increased with luminance contrast (SLR: $a = 2.19e-2$; CI = $5.22e-3$; Figure 4F). The PSPC latency decreased with luminance (SLR: $a = -0.480$; CI = 0.156 ; Figure 4C). As a result of the effects of luminance on PSPC latency and PSPC velocity, the time to reach the maximum constriction was independent of luminance (SLR: $a = 0.419$; CI = 0.212 ; Figure 4E).

Discussion

These results showed that after a PS, several parameters of pupil dynamics were correlated with the luminance level at the landing position, (i.e., the fixated disk), including initial pupil dilation, average pupil size, constriction amplitude, and constriction velocity, but not the latency of the maximum constriction. These results confirm that pupil responses are mostly driven by central vision.

In line with previous studies (Fukuda, Stern, Brown, & Russo, 2005; Jainta, Vernet, Yang, & Kapoula, 2011;

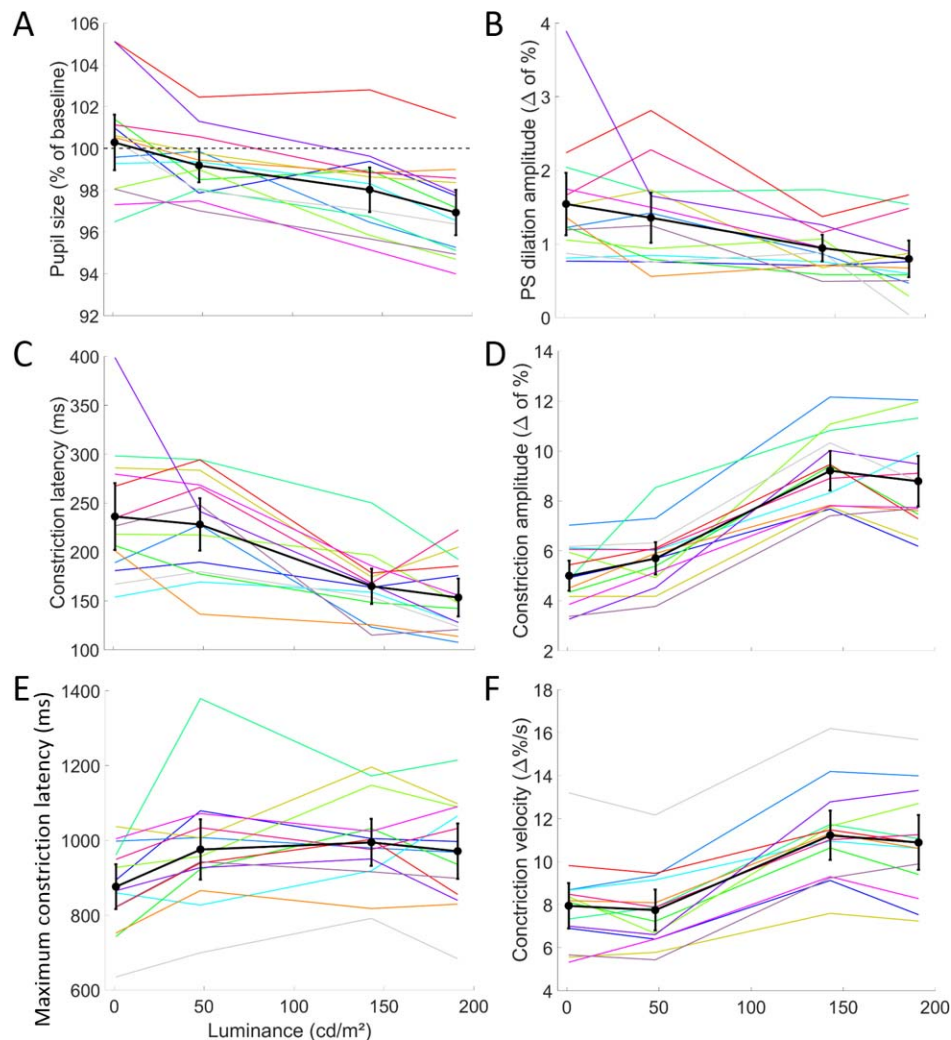


Figure 4. Effect of the luminance of the gazed disk on pupil dynamics. Black filled circles represent the average across participants; black error bars show the 95% CI of the population. (A) Mean pupil size (in percentage of baseline); (B) postsaccadic dilation amplitude; (C) PSPC latency; (D) postsaccadic pupil constriction amplitude; (E) latency of maximum constriction; (F) constriction velocity (in percentage of base line per s).

Wang, Boehnke, Itti, & Munoz, 2014), we observed a small pupil dilation after a PS, followed by a constriction whose amplitude, latency, and velocity depend on the luminance of the fixated region. A recent study suggests that this dilation reflects the activity in and from the superior colliculus where microstimulation can elicit dilation of the pupil whose amplitude is larger on a dim as compared to a bright background (Wang, Boehnke, White, & Munoz, 2012). These authors suggest that this initial postsaccadic pupil dilation reflect an orienting preparatory activity to future incoming stimuli.

Finally, the effects of the luminance level on pupil responses seem to saturate for the highest luminance, in line with the known pupil/luminance response function (Chung & Pease, 1999; Clarke et al., 2003).

In Experiment 1, pupil size was mainly driven by the luminance level present in central vision. The

attentional load was low and solely related to the sounds triggering PS, with no other task than fixating the center of a disk. Quantitatively assessing the possibility that changes of the eyes' optics (linked to pupil responses during scene exploration) modulate visual processing, requires performing a visual task and evaluating perceptual performance. This task, whatever it is, will modulate the attentional load, which should itself modulate pupil size, mostly by eliciting pupil dilation (Kahneman et al., 1967; Beatty & Wagoner, 1978). To characterize pupil dynamics in this case, Experiment 2 uses stimuli similar to those of Experiment 1, but a difficult spatial discrimination task was added to evaluate whether, and to what extent, pupil size modulates behavioral performance, and or whether the attention load modulates pupil responses during the fixation of disks at different luminance levels.

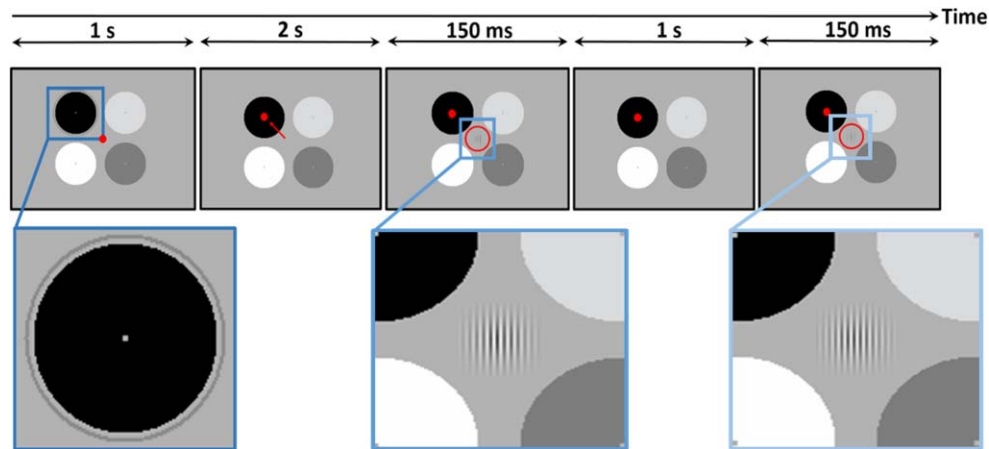


Figure 5. Experiment 2: Design and time course. For illustrative purposes, red points and red arrows indicate the sequence of fixations. The red circles show the timing and location of the Gabor patches to be discriminated. A trial began with a central fixation during 1 s (as in Experiment 1). A gray circle (80 cd/m^2) surrounding the disk to fixate during the trial was then presented during 1 s to trigger a saccade. After 2 s of fixation, a Gabor patch was flashed at the screen center for 150 ms, followed, after 1 s, by a second Gabor patch with a different spatial frequency. Participants had to indicate which Gabor had the highest spatial frequency using a 2IFC design.

Experiment 2: Spatial frequency discrimination with varying pupil size

Experiment 2 aims at testing whether pupil size, which depends on the luminance of a gazed target (as shown in Experiment 1), influences performance in a spatial frequency discrimination task. It is expected that behavioral performance should be better when pupil size is small, (i.e., when fixating a high luminance target), than when pupil size is large, (i.e., during fixation of a low luminance target), due to changes in the eye's optic quality (Campbell & Gregory, 1960; Campbell & Gubisch, 1966).

As, however, this discrimination task engages attention, a second hypothesis is that pupil dynamics and averaged pupil size will also be modulated by attention.

Stimulus and procedure

The stimuli used in Experiment 2 were the same as Experiment 1. Because this experiment required performing a discrimination task, the procedure was slightly adapted to meet this constraint: a single target configuration was used (the one represented on Figure 1). The sound cue was replaced by a visual cue: a circle of low contrast around the target disk appeared during 1 s at the beginning of the trial (Figure 5).

A trial comprised only one fixation of one of the four disks lasting about 4 s, during which two Gabor's

patches (sigma: 1.7° , vertically oriented spatial frequency gratings: 9 and 9.7 c/° , Michelson contrast: 0.99) were flashed in succession in random order at the center of the monitor for 150 ms with a 1 s interval between both (Figure 5). The choice of these spatial frequencies was based on previous results (Campbell et al., 1970; Berkley, Kitterle, & Watkins, 1975) as they are close to the spatial discrimination threshold in this frequency range. Participants were instructed to fixate the cued fixation disk throughout the trial, and to avoid saccades toward the Gabor's patches. At the end of each trial, participants had to indicate which of the two Gabor's patches had the highest spatial frequency by pressing a one of two keyboard keys (two-interval forced-choice design, 2IFC). The button press triggered the beginning of the next trial. There were four conditions (four disks with luminance levels as in Experiment 1). Each condition was repeated 60 times in three sessions of 80 trials. This second experimental session was performed the same day as Experiment 1.

Data analysis

Overall, the analyses followed the same steps as Experiment 1. Trials during which a blink or a saccade occurred 0.25 s before the presentation of the first Gabor patch, or 0.25 s after the end of the presentation of the second Gabor patch, were excluded. The same variables as those of Experiment 1 were computed and analyzed in the same way. The effects of the Gabor patches flashes on pupil responses were also analyzed to determine whether they elicited pupil responses. In addition, we compared the slopes of pupil dynamics

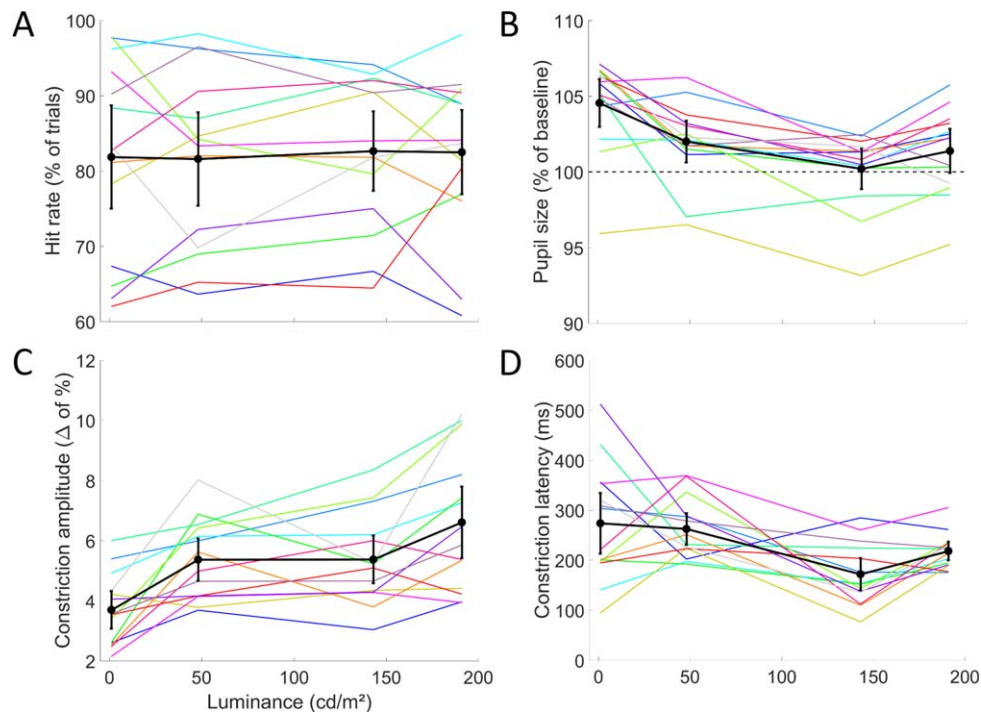


Figure 6. Results of Experiment 2: Black filled circles represent the average across subjects and black error bars show the 95% CI; colored lines represent the averaged results of each subject. (A) Performance in the spatial frequency discrimination task as a function of luminance. (B) Normalized pupil size as function of luminance; dashed black line: baseline pupil size. (C) PSC amplitude in percent of baseline pupil size. (D) Average latency of the beginning of PSC.

500 ms before and 500 ms after each Gabor flash onset. The parameters of pupil dynamics were compared to performance in the discrimination task. To that aim a logistic regression was computed by pooling data of all subjects and conditions; we present as follows the equations corresponding to the resulting predictions together with their associated p value. Cohen's d values were used to compare the variables of interest measured in Experiment 1 and Experiment 2.

Results

We first analyzed the eye movements made during fixation, removing the trials where participants did not maintain their gaze within a 1° window centered on each target disk. Using this criterion led to the removal of 16.07% of the trials (see Supplementary Figure S2F).

Effects of luminance on pupil dynamics

Overall, the time course of pupil size during a trial was similar to that observed in Experiment 1 (Figure 6 and Supplementary Figure S3–S5), with, however, some noticeable differences analyzed thereafter. Importantly, we did find larger and faster pupil constrictions when participants fixated disks with high, as compared to low, luminance, allowing testing the

hypothesis according to which pupil size modulates spatial discrimination performance. Performance in the spatial frequency discrimination task was highly variable across participants, ranging from $\sim 60\%$ to $\sim 95\%$ (Figure 6A). However, we did not find significant effects of luminance, and thus of pupil size, on performance (SLR: $a = 5.43e-5$; CI = $1.89e-4$; Figure 6A).

We further analyzed pupil dynamics as in Experiment 1. We observed a medium effect size of the luminance level on averaged pupil size (SLR: $a = -1.69e-2$; CI = $4.85e-3$; Figure 6B). Pupil size decreased with increasing luminance of the gazed disk. The variance of pupil size during fixation was not correlated to disk luminance and decreased with increasing luminance (average and 95% CI in percentage of baseline: 1 cd/m^2 : 4.57 ± 0.67 , 48 cd/m^2 : 3.71 ± 1.01 ; 143 cd/m^2 : 4.08 ± 0.89 , 191 cd/m^2 : 3.97 ± 1.05 ; SLR: $a = -1.71e-3$; CI = $1.06e-3$; data not shown). Figure 6C shows the amplitude of the PSC, which increased with luminance (SLR: $a = 1.21e-2$; CI = $3.85e-3$). PSC latency was shorter (SLR: $a = -0.417$; CI = 0.237 ; Figure 6D) and pupil constriction was faster at high, compared to low, luminance (average and 95% CI in %/ms: 1 cd/m^2 : 8.26 ± 1.86 , 48 cd/m^2 : 9.63 ± 2.30 ; 143 cd/m^2 : 9.29 ± 1.78 , 191 cd/m^2 : 10.66 ± 3.09 ; SLR: $a = 1.22e-2$; CI = $5.04e-3$; data not shown).

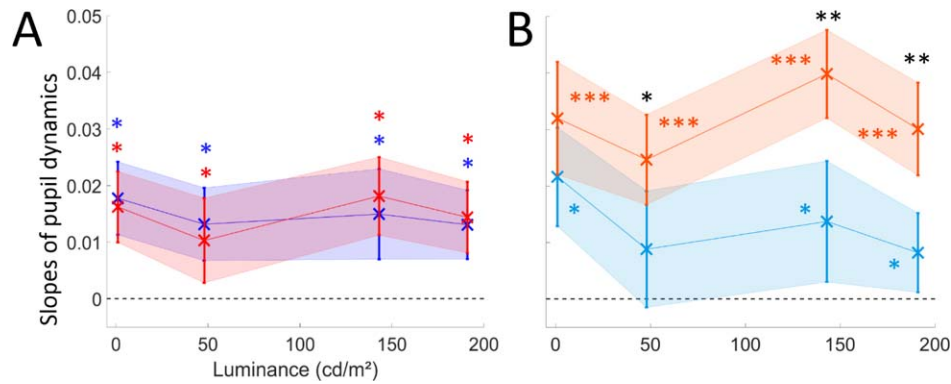


Figure 7. Pupil dynamics during stimulus encoding. (A) Average across subjects and 95% CI of the slopes computed 500 ms before (blue) and 500 ms after (red) the first Gabor onset. Positive slopes indicate pupil dilation. Student's t tests and Cohen's d show no significant difference between the pupil slopes before and after the 1st Gabor onset. Red and blue asterisks indicate when the averaged slopes were different significantly from zero: Student's t test *: $p < 0.05$. (B) Same as (A) for the second Gabor onset (light blue: 500 ms before; orange: 500 ms after Gabor onset). Orange and light blue asterisks indicate the conditions for which the averaged slopes were different from zero: Student's t test * $p < 0.05$; *** $p < 1e-4$. Significant differences between slopes before and after the Gabor flash are shown with black asterisks: * Student's t test, $p < 0.01$ and Cohen's $d > 0.5$; ** Student's t test, $p < 0.005$ & Cohen's $d > 1$.

Effects of the Gabor stimuli on pupil responses

To test whether the presentation of the Gabor stimuli elicited any specific pupil activity, we computed the slopes of pupil modulation 500 ms before and 500 ms after the presentation of each of the two Gabor stimuli, for each luminance level (Figure 7A, B). We did not observe significant pupil constrictions in response to any of the 150 ms Gabor flashes (Figure 7A, B), as the slopes were positive, showing that the pupil dilated during these time windows. Comparing the pupil dilation slopes before and after the presentation of the first Gabor flash or in between the two Gabor presentations revealed no significant changes for these time windows (Figure 7A). In contrast, the dilation slopes following the presentation of the second Gabor patch were steeper than the slopes measured 500 ms before the presentation of the second Gabor stimulus, except for the lowest luminance level (Figure 7B). We further observed that the dilation slopes after the second Gabor flash are larger at a high, as compared to a low, luminance level, presumably because the pupil was already dilated when fixating a dark, as compared to a bright disk, such that the pupil, being more constricted, could dilate faster in this latter case.

Pupil dilation and perceptual performance

We then examined whether behavioral performance was correlated with pupil dynamics. Figure 8A–D shows the distributions of the slopes computed on each 500 ms time window across subjects and luminance conditions. To determine how well these slopes allow predicting behavioral performance, we used a logistic regression using the responses to the task and the slopes

of pupil activity during each of the four time intervals. Figure 8E shows predicted performance as a function of the dilation slopes. As it can be seen, the slopes of pupil dilation during the presentation of the two Gabor stimuli allows predicting performance with better accuracy (after the first Gabor: $p = 0.059$; before the second Gabor, $p < 0.001$) than the slopes computed before or after the presentation of the Gabor stimuli (before the first Gabor, $p = 0.711$; after the second Gabor $p = 0.541$). The distribution of hit rates as a function of the slopes of pupil activity for each participant is presented in Supplementary Figure S6.

These results indicate that faster pupil dilation during information encoding (i.e., encoding the relative spatial frequency of the Gabor patches) predicts more accurate performance than pupil dilation before information encoding or during decision-making.

Comparison between Experiment 1 and 2

Pupil data collected in Experiments 1 and 2 present similarities and dissimilarities that we describe and analyze thereafter. As a first approximation, we assumed that comparing the results of the two experiments is valid because the same participants performed the two experiments in a single session and because the stimuli were the same. We present the observed differences in pupil dynamics before discussing methodological differences between the two experiments that could argue against the mere possibility to make such comparisons.

In Experiment 2, the average pupil size was significantly larger than in Experiment 1 (Figure 9A).

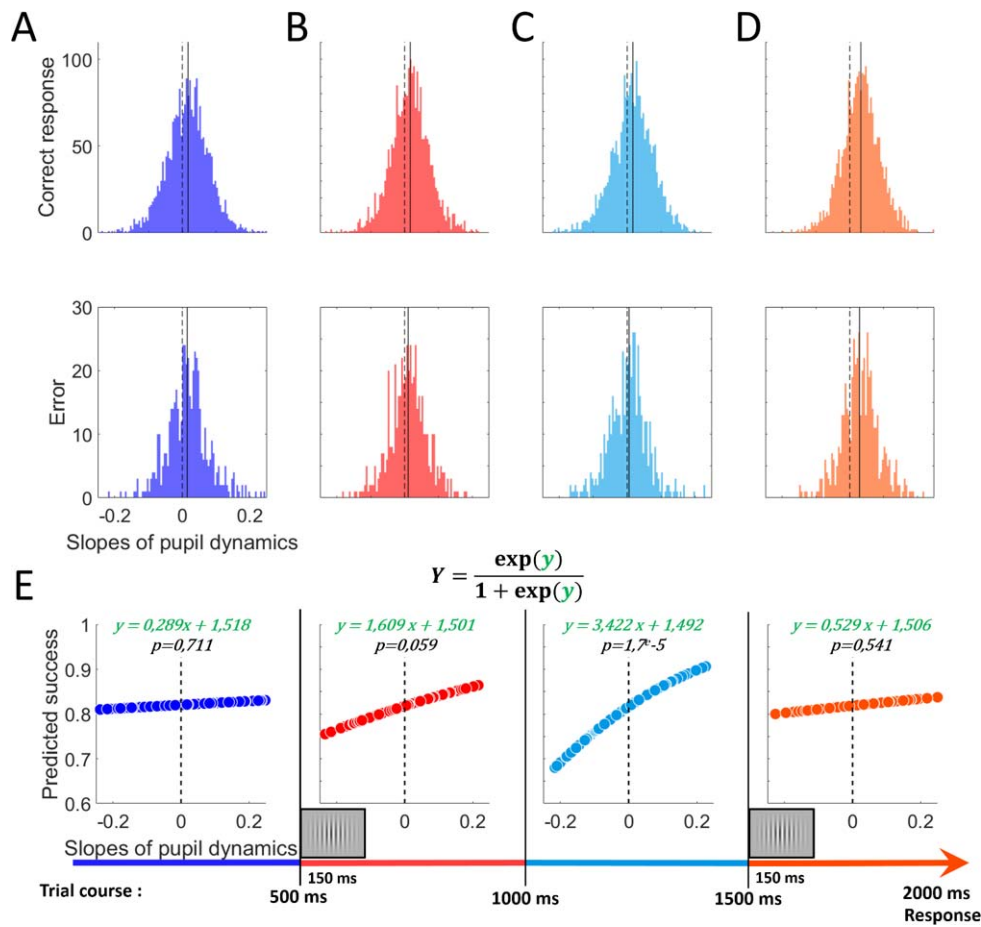


Figure 8. (A–D). Distributions of the slopes of pupil dynamics for correct discrimination and errors at different 500 ms time windows. Dashed lines represent a null slope; thick lines show the medians of the distributions. (A) before the presentation of the first Gabor (blue), (B) after the presentation of the first Gabor (red), (C) before the presentation of the second Gabor (light blue), (D) after the presentation of the second Gabor (orange). (E) Performance predicted by a logistic regression of the slopes pooled across subjects and conditions as a function of pupil slopes. The coefficients of the equations of the general linear model and the corresponding p values are shown for each time window. Positive pupil slopes (right of the vertical dashed lines) indicate a dilating pupil.

Comparing the PSC amplitude reveals differences with a large effect size, for three out of four luminance levels, with smaller constriction amplitude in Experiment 2 as compared to Experiment 1 (Figure 9B). The PSC latency also differed between the two experiments, but only for the highest luminance level, increasing with a high effect size in Experiment 2 relative to Experiment 1 (Figure 9C). Finally, PSC was significantly faster for the dark gray target and slower for the light gray target in Experiment 2 as compared to Experiment 1, with high effect size (Figure 9D).

These differences are puzzling because they appear heterogeneous across luminance levels, with no trivial explanation. In particular, the observation that some differences are larger for the extreme luminance (averaged pupil size and PSC latency) than for the intermediate luminance levels (PSC amplitude and PSC velocity) seems odd. Nevertheless, an account of these differences could be as follows: adding a task in

Experiment 2 changes the overall cognitive load. This should alter the balance between the sympathetic and parasympathetic pathways, possibly through an inhibition from the sympathetic pathway onto the Edinger-Westphal nucleus (Merritt et al., 2004; Wang et al., 2012). With an added task, the pupil is less reactive to external stimulation because of this inhibitory drive, resulting in a smaller and slower constriction and in increased constriction latency. One account of the effect of luminance is that the luminance level “clamps” the pupil to different degrees, letting or not letting room for an attentional and or a cognitive influence.

However, some methodological differences between the two experiments weaken the validity of the comparisons between Experiment 1 and 2. In Experiment 1, a sound was used to trigger saccades to a different target disk, and a trial consisted in four successive fixations of 2 s each. In Experiment 2, a low luminance circle surrounding a target disk was used to trigger saccades to

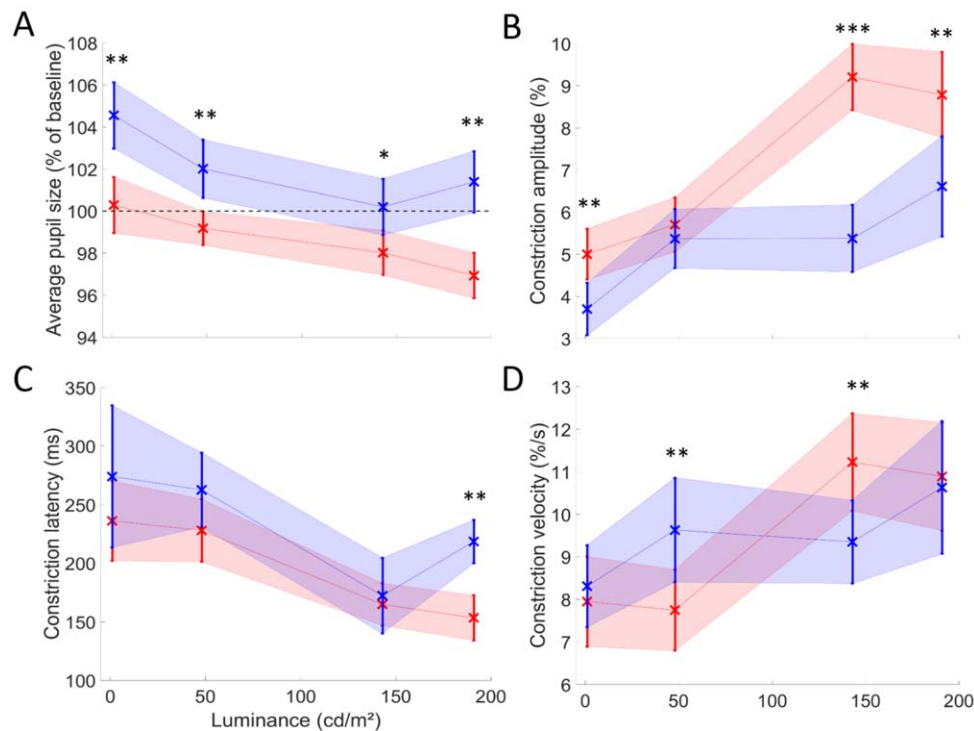


Figure 9. Comparison of Experiment 1 (red) and 2 (blue). Crosses represent population average. Error bars represent the 95% CI and the asterisks represent the significance of difference between both experiments (*Cohen's $d < 0.5$; ** $d > 1$; *** $d > 2$). (A) Average pupil size in percentage of the baseline. (B) PSPC amplitude in percentage of baseline. (C) PSPC latency. (D) PSPC velocity.

the target disks. In addition, to include a spatial frequency discrimination task, a trial, lasting 3,300 ms, consisted in a single fixation on one of the four disks during which two Gabor patches, to be discriminated, were flashed for 150 ms at 1 s interval. These differences may account for some of the differences between the results of Experiment 1 and 2, and limit the conclusions that can be drawn. Despite these differences, the relative effect of the luminance of the fixated targets measured in the two experiments remains relevant.

Discussion

We performed two experiments to examine (1) to what extent the size of the pupil depends on the luminance of a gazed stimulus in an otherwise unchanging display, and (2) to test whether pupil size which determines the eyes' optics, influences visual performance in a spatial frequency discrimination task. Although we did find that pupil size depends on the luminance of centrally fixated regions, we did not find any effect of pupil size on visual discrimination performance. This finding goes against our initial assumption that changes in pupil size modify the optics of the eyes in a way that impact visual performance. Despite this, we found correlations between pupil

dynamics and visual performance that replicate, and extend, previous findings. In particular, the use of a 2IFC design allowed distinguishing the periods of visual information encoding from that related to accumulation evidence and perceptual decision-making. We now discuss both aspects of our results: lack of improvement of visual performance with high luminance disks that elicit a pupil constriction, and the dynamics of pupil dilation in relationship to performing a perceptual task, independently of the luminance conditions.

Effect of luminance and pupil size on behavioral performance

Our results appear at odds with conclusions from previous studies. The seminal studies of Campbell and Gregory (1960) assessed the expected effect of pupil size on the detection threshold of spatial frequency gratings, and the concomitant changes of the point spread function (Campbell & Gubisch, 1966). However, these studies were conducted with artificial pupils of fixed and well-controlled size, after a physiological induction of pupil dilation with drugs. In these conditions, any physiological pupil size fluctuation that could occur while performing the task is eliminated, such that the diameter of an "artificial pupil," and thus the eyes' optics, remain the same throughout a trial.

To our knowledge, no demonstration of the effects of pupil size on visual performance with natural pupils has been performed since, maybe because the pupil is never at rest and greatly varies over time, such that the optic quality of the eyes also constantly varies.

In this regard, it is worth noting that the time course of the pupil responses after a PS was overall slow (the average latency to reach the maximum constriction was about 900 ms after a PS in Experiment 1). As, on average, individuals make about 3 saccades/s (about 330 ms fixation in-between saccades), pupil responses to local parafoveal luminance levels cannot fully develop, such that it seems unlikely that changes in the eyes' optics related to pupil size modulation can significantly influence visual processing in everyday life.

In the present experimental conditions with long fixations, assuming that spatial frequency discrimination relies on the differential cortical activity elicited by different spatial frequencies, our findings are compatible with a recent study (Thigpen, Bradley, & Keil, 2018) showing that modulations of pupil size do not correlate with changes of cortical activity, as measured with steady state visually evoked potential. In contrast, another study (Bombeke, Duthoo, Mueller, Hopf, & Boehler, 2016) reports a correlation between both. Large differences in methods and stimuli may explain the discrepancy between these studies. One notable difference concerns the task given to the participants. In the study of Thigpen et al. (2018), observers “were told to look at any stimuli that appeared on the screen”, with no attempt to modulate or control attention, while “participants had to covertly orient their attention to the white or black disk on a given trial. Participants were told to keep accurate fixation and to minimize blinking” in the study of Bombeke et al. (2016, Experiment 1). This difference may have important consequences on the motility and dynamics of the pupil, in particular regarding the inhibition exerted by the sympathetic pathway onto the Edinger-Westphal nucleus (Merritt et al., 2004; Wang et al., 2012). Mobilizing attention to perform a particular task in the laboratory, which is rarely the case in natural viewing conditions where endogenously generated “tasks” that accompany “seeing” are continuously changing over time, may modulate pupil reactivity as well as cortical processing and perceptual performance.

In line with the seminal work of Beatty (1982) and others, recent studies (Mathôt et al., 2013; Binda & Gamlin, 2017) reported that covertly attending to a bright stimulus modulates pupil size according to the luminance of the attended target. In agreement with these previous studies, our data show that the pupil light reflex occurring after a saccade toward a new location is not exclusively driven by parasympathetic inputs, and is balanced by sympathetic inputs reflecting the cognitive load brought by a visual task. This may be

important when considering clinical assessments of visual acuity or pupil activity to diagnose retinal pathologies, as the settings used in clinical tests are similar to those used in the laboratory. The lack of control and evaluation of cognitive states (stress, fatigue, mind wandering, attention, etc.) may limit the sensitivity and specificity of these tests, especially those relying on the pupil light reflex.

Pupil dynamics during 2IFC spatial frequency discrimination

Numerous studies reported that the pupil dilates after detecting a stimulus at threshold (Hakerem & Sutton, 1966; Kahneman et al., 1967), when detecting a target in a flux of irrelevant distracters (Beatty & Wagoner, 1978; Privitera et al., 2008; de Gee et al., 2014), during memory encoding (Beatty, 1982; Kucewicz et al., 2018) or in relationships with decision-making (Einhauser et al., 2010; Preuschoff et al., 2011; de Gee et al., 2014). In these latter studies, a spatial two-alternative forced choice design, using a single stimulus presentation, is often used (but see De Gee et al., 2014).

Measuring spatial frequency discrimination with a 2IFC design, as done here, allowed separately analyzing the stimulus encoding period, during which no decision can be made, from a period related to the building up of a perceptual decision. The analyses conducted on the slopes of pupil dilation computed on different time windows revealed that the slopes of pupil dilation during stimulus encoding were positively correlated to individual performance, while the dilation slopes occurring after the encoding of the two stimuli were not. Although this lack of correlation may seem surprising, we note that the need to provide an answer in a perceptual task engages several processes related to decision making (evidence accumulation, decision, motor preparation, and execution), whatever the quality and reliability of the evidence available after information encoding. These different processes are known to be cognitively demanding and to induce a pupil dilation related to the activation of the sympathetic pathway, but the present results showed that mobilizing these different processes is not necessarily a guarantee to yield a correct answer. Our study demonstrate that pupil dilation during information encoding, reflecting increased attention to the targets, is a better predictor of performance than the pupil dilation occurring after stimulus encoding, related to decisional processes. This finding is in agreement with previous studies on memory, showing that pupil dilation during stimulus encoding predicts the success of delayed recall (Kahneman et al., 1967; Starc, Anticevic, & Repovš, 2017; Kucewicz et al., 2018).

Conclusion

The extensive analyses performed on our data set show that pupil size continuously fluctuates over time, with very large intra- and inter-individual differences. Gaze-dependent modulations of pupil size, and consequently of the eyes' optics, are uncorrelated to visual performance and appear too variable—in time, within and across individuals—to significantly influence visual processing, at least the spatial discrimination of high spatial frequency stimuli, as measured in this study. Whether pupil dilation linked to cognitive factors plays a functional role in visual perception remains a matter of debate. Several effects of changes of pupil size have been considered, but they often have opposite effects: increasing the quantity of light entering the eyes with large pupils may improve overall visual sensitivity, but reduces the spatial resolution that can be achieved. Another intriguing possibility is that large pupils reduce the depth of field, such that objects far from the attended plane are blurred, which might improve the segregation of different depth planes encountered in cluttered environments.

To conclude, we note that studying the effects of pupil size and eyes' optics on visual perception faces the caveat that an explicit task has to be used. Introducing such a task engages attention and creates a situation where pupil dynamics is modulated by the task itself, presumably through a sympathetic neuromodulation of pupil activity. This limits the mere possibility of evaluating the effects of pupil size on visual perception in natural situations, where visual tasks performed by individuals are most often implicit.

Keywords: pupil, luminance, eyes' optics, attentional load, spatial discrimination

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Corrected October 31, 2018: The phrase “We further observed that the dilation slopes after the second Gabor flash are larger, as compared to low, luminance level” was changed to “We further observed that the dilation slopes after the second Gabor flash are larger at a high, as compared to a low, luminance level.”