

Pupil size is modulated by the size of equal-luminance gratings

Jie Gao

Key Laboratory of Brain, Cognition and Education Sciences, Ministry of Education; Center for the Study of Applied Psychology; Guangdong Key Laboratory of Mental Health and Cognitive Science, School of Psychology, South China Normal University, Guangzhou, Guangdong Province, China



Athena Ko

Brain and Mind Institute, The University of Western Ontario, London, Ontario, Canada



Yoshiko Yabe

NTT Communication Science Laboratories, Nippon Telegraph and Telephone Corporation, Atsugi, Kanagawa, Japan



Melvyn A. Goodale

Brain and Mind Institute, The University of Western Ontario, London, Ontario, Canada
Department of Psychology, The University of Western Ontario, London, Ontario, Canada



Juan Chen

Key Laboratory of Brain, Cognition and Education Sciences, Ministry of Education; Center for the Study of Applied Psychology; Guangdong Key Laboratory of Mental Health and Cognitive Science, School of Psychology, South China Normal University, Guangzhou, Guangdong Province, China



Pupil size changes with light. For this reason, researchers studying the effect of attention, contextual processing, and arousal on the pupillary response have matched the *mean* luminance of their stimuli across conditions to eliminate the contribution of differences in light levels. Here, we argue that the match of mean luminance is not enough. In Experiment 1, we presented a circular sinewave grating on a gray background for 2 seconds. The area of the grating could be 3°, 6°, or 9°. The mean luminance of each grating was equal to the luminance of the gray background, such that regardless of the size of the grating there was no change in mean luminance between conditions. Participants were asked to fixate the center of the grating and passively view it. We found that in all size conditions, there was a pupil constriction starting at about 300 ms after stimulus onset, and the pupil constriction increased with the size of the grating. In Experiment 2, when a small grating was presented immediately after the presentation of a large grating (or vice versa), the pupil constriction changed accordingly. In Experiment 3, we replicated Experiment 1 but had the subjects perform an attention-demanding fixation task

in one session, and passively view the stimuli in the other. We found that the main effect of task was not significant. In sum, our results show that stimulus size can modulate pupil size robustly and steadily even when the luminance is matched across the different stimuli.

Introduction

Pupil size changes with light; the pupil constricts when the stimulus is bright and dilates when the stimulus is dark. This fast and sensitive response to light is believed to be mediated by a subcortical system. It has been shown, however, that a change in pupil size reflects not only this “reflexive” response to light but also high-level sensory and cognitive processing. For example, pupil size is modulated by perceived luminance, not just physical luminance, and can reflect the high-level content of an image (Naber & Nakayama, 2013). Moreover, it can even

Citation: Gao, J., Ko, A., Yabe, Y., Goodale, M. A., & Chen, J. (2020). Pupil size is modulated by the size of equal-luminance gratings. *Journal of Vision*, 20(8):4, 1–9, <https://doi.org/10.1167/jov.20.8.4>.



indicate perceptual selection in a bistable stimulus (Einhäuser, Stout, Koch, & Carter, 2008). In addition, the pupillary response has also been used as a predictor of blindsight in hemianopia and can serve as a conduit for communication with locked-in patients (Sahraie, Trevethan, MacLeod, Urquhart, & Weiskrantz, 2013; Stoll et al., 2013; Weiskrantz, Cowey, & Barbur, 1999). Pupil size is also modulated by, for example, attention (Binda & Gamlin, 2017; Binda, Pereverzeva, & Murray, 2013a; Binda, Pereverzeva, & Murray, 2014; Gabay, Pertzov, & Henik, 2011; Kang, Huffer, & Wheatley, 2014; Wierda, van Rijn, Taatgen, & Martens, 2012; Willems, Damsma, Wierda, Taatgen, & Martens, 2014), affection (Partala & Surakka, 2003), and emotional memory (Sterpenich et al., 2006).

Because the luminance of the stimuli may affect the results of cognitive and perceptual experiments that use pupil size as a dependent measure, researchers typically employ ways of ruling out the confound of luminance levels on the main findings (Binda, Pereverzeva, & Murray, 2013b; Sperandio, Bond, & Binda, 2018; Sterpenich et al., 2006). For example, researchers have used the phase-scrambled but luminance-matched version of the same stimulus as a control (Binda et al., 2013b) or have used an inverted version of the stimuli as a control so that the mean luminance is matched but the meaning of the picture is no longer readily available (Naber & Nakayama, 2013). In another example, Laeng & Endestad (2012) examined the pupil constriction induced by visual illusions. Given that the pictures with the illusion or without the illusion were different in mean luminance or the distribution of luminance, they matched the overall luminance of the stimuli by displacing or translating the elements or changing the size of the inducing shapes.

Some of these ways of ruling out the confound of luminance level may not be as valid as expected because, besides luminance, other visual features including contrast, spatial frequency, color, movement (Barbur & Thomson, 1987; Slooter & van Norren, 1980; Ukai, 1985), and the eccentricity of the stimulus (Barbur & Thomson, 1987) can also modulate the pupil response. This suggests that controlling for possible differences in luminance should not introduce changes in these features when designing the control stimuli. For example, a phase-randomized version of an image might not be a perfect control because a bright part presented in the periphery may be moved to the center of the visual field in the phase-scrambled version which could introduce changes in pupil size due to the changes in eccentricity. This confound could be ruled out, however, if the same manipulation was carried out across all different stimuli and conditions.

Here, we show that the change in stimulus size will also affect pupil size even when the mean luminance is constant (equal luminance). To this end, we presented gratings of different sizes but with the same mean

luminance as the background. In Experiments 1 and 2, we examined whether the grating size influences pupil size (the larger the grating, the larger the pupil constriction) and whether the pupil constriction for each size depends on the order of presentation. In Experiment 3, we examined whether attention modulates the effect of grating size on pupil size. Our results suggest that one should be cautious when changing the size of the stimulus to control for overall luminance in experiments that use pupil size as a measure (Laeng & Endestad, 2012).

Materials and methods

Participants

Six naïve students (three females and three males, mean age = 20.78 years) participated in both Experiments 1 and 2. A new group of seven participants (five females and two males, mean age = 23.14 years) participated in Experiment 3. All participants had normal or corrected-to-normal vision. They were naïve to the purpose of the experiments, and they gave written informed consent. The experiment was approved by the ethics committee of the University of Western Ontario.

Apparatus

The stimulus was presented on a cathode-ray tube (CRT) monitor (resolution, 1024 × 768; refresh rate, 100 Hz; ViewSonic, Brea, CA). The distance from the eyes to the monitor was 86 cm. The presentation of stimuli was controlled by Psychtoolbox 3 (Brainard, 1997) embedded in MATLAB 2014 (MathWorks, Natick, MA). The monitor was turned on at least 1 hour in advance of the experiment for each participant so that the luminance of the monitor was stabilized. To confirm that the luminance of the monitor was indeed stable, we measured the luminance of the monitor (Konica Minolta LS-100 Luminance Meter; Konica Minolta, Tokyo, Japan) before and after each participant's testing session for grayscales that ranged from 0 to 255 with a step of 15 in a random order (Figure 1A, Experiments 1 and 2; Figure 1B, Experiment 3). The mean differences in luminance measured before and after the testing sessions, averaged across the grayscales and participants, were 0.014 cd/m² for Experiments 1 and 2 and 0.072 cd/m² for Experiment 3. (Note that Experiments 1 and 2 were performed in one session, and Experiment 3 was performed in a separate session.) This suggests that the luminance of the monitor was stable throughout each testing session. Gamma correction was done for each experiment to compensate for the CRT monitor's nonlinear response to the input signal

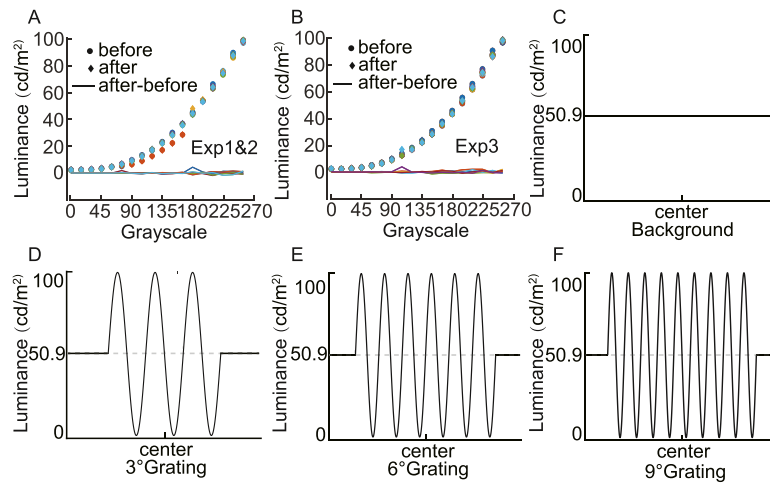


Figure 1. Luminance of the screen (A and B), luminance of the gray background (C), and luminance of the gratings of different sizes perpendicular to its orientation (D–F). (A, B) Luminance values of grayscales from 0 to 255 with a step of 15 before and after each test (A for Experiments 1 and 2; B for Experiment 3) are shown with each symbol for each participant. The lines of different colors show the difference in luminance before and after each test for each participant. (C) Luminance of blank screen that was set to the luminance of the gratings. (D–F) The luminance for gratings of 3°, 6°, and 9° perpendicular to the orientation of the gratings. For vertical gratings, these curves show the luminance along the horizontal direction; for horizontal gratings, these curves show the luminance along the vertical direction. The luminance along the orientation of the grating is constant.

(i.e., grayscale values). Pupil area was measured via a video-based infrared eye tracker (EyeLink 1000 tower mount; SR Research, Ltd., Kanata, ON, Canada) at a sampling rate of 1000 Hz with monocular recording (right eye). The testing area where the participant, the EyeLink tower, and the CRT monitor were located was shielded from light, and the hosting computer and recording monitor were located outside this area.

Experiment 1

Stimuli

The purpose of this experiment was to test whether or not pupil size is modulated by grating size even when the mean luminance of the gratings is kept constant. Three sizes of circular sine-wave gratings (3°, 6°, and 9°; luminance range, 2.15 cd/m² to 99.68 cd/m²; spatial frequency, 1 c/°) were presented in the center of a gray screen (mean luminance, 50.92 cd/m²) (Figure 1A). Two orientations, vertical and horizontal, were presented randomly in each block of trials. For horizontal or vertical gratings, the luminance was constant along one direction but changed according to the sine-wave function along the perpendicular direction. Theoretically, the areas of white, gray, and black were balanced (Figures 1D–1F), and the mean luminance was constant regardless of grating size, as long as the grating consisted of an integral multiple of cycles. We set the luminance of the background to be

the mean luminance of the grating (Figure 1C), which guaranteed that the mean luminance level during the trial remained unchanged with and without stimulus presentation, and there was never a change in overall luminance caused by the presentations of the grating.

Design and procedure

The experiment consisted of eight runs, 12 trials per run. Calibration and drifting correction were done at the beginning of each run. Before each trial, participants were asked to maintain fixation on a green fixation point presented in the center of the screen and to avoid blinking as much as possible. When they were able to maintain fixation, the experimenter pressed a computer key to trigger the start of each trial and the recording of the pupil area. Right after the keypress, the fixation point was first presented for 0.5 second followed by a grating (3°, 6°, or 9°) for 2 seconds (Figure 2A). Participants did not perform any task other than maintaining fixation.

Experiment 2

Stimuli

Two (3° and 9°) out of the three gratings that were used in Experiment 1 were used in this experiment. Again, the mean luminance of each grating was

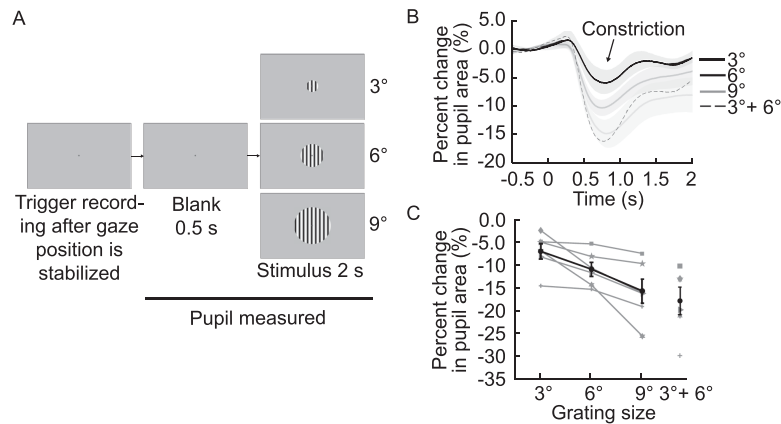


Figure 2. Stimuli, protocol, and results for Experiment 1. (A) On each trial, participants were asked to maintain fixation on the center of the screen. After the participant's gaze position stabilized, the experimenter pressed a key to trigger the recording of pupil area. About 0.5 second after the key was pressed, a stimulus of 3°, 6°, or 9° was presented for 2 seconds. (B) The profile of percent change in pupil area averaged over all participants for each condition; the shaded area shows the standard error. (C) The peak of the profiles obtained in B for each participant (gray lines with symbols) and their average (black line with error bars) for each condition. The error bars show $1 \pm SE$. The symbols on the right show the sum of the pupil changes to the 3° and 6° gratings for each participant.

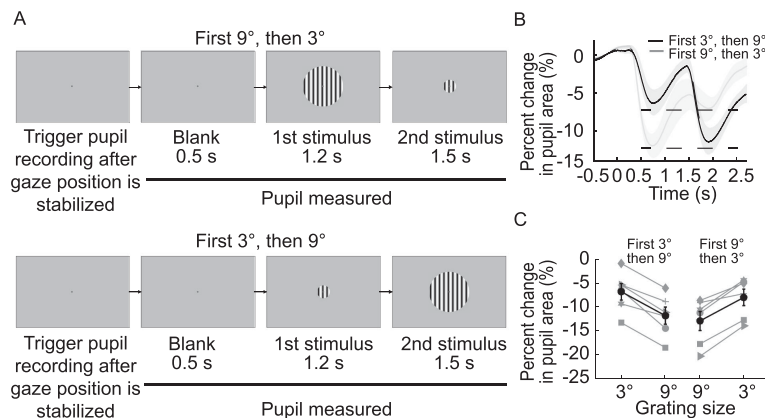


Figure 3. Stimuli, protocol, and results of Experiment 2. (A) In one condition, the large grating was presented and followed by the smaller one; in the second condition, the small grating was presented first followed by the larger one. (B) The profile of the percent change in pupil area in both conditions; the shaded area shows the standard error. (C) The peak pupil constriction for each participant in each condition.

matched to the luminance of the gray background. The viewing distance was also 86 cm.

Design and procedure

The procedure of Experiment 2 was similar to that of Experiment 1, except that the two gratings were presented successively. The purpose of this experiment was to determine whether pupil size would follow rapid changes in the size of the equal-luminance gratings and whether the change in pupil size depends on the presentation order of the stimulus. To do this, we included two conditions. In one condition, the 3°

grating was presented first, followed by the 9° grating; in the other condition, the 9° grating was presented first. The first grating was presented for 1.2 seconds; the second for 1.5 seconds. The experiment consisted of three runs, 18 trials per run, and nine repetitions of each condition within each run. The order of the two conditions was randomized within each run. Again, the experimenter triggered the start of each trial and the recording of the pupil area after the participant's gaze position was stabilized. Pupil area was recorded until the second stimulus disappeared (Figure 3A).

Participants performed Experiments 1 and 2, together with a control experiment (five out of the

six participants performed this control experiment), in one session which took 1.5 to 2 hours in total. The control experiment replicated previous finding that the spatial frequency of a equal-luminance grating modulates pupil constriction (Barbur & Thomson, 1987), which indicated that our equipment, the data acquisition, and analysis were working properly.

Experiment 3

Stimuli

The same gratings used in Experiment 1 were also used in Experiment 3. The main difference between displays was that, in Experiment 3, a series of letters (Z, L, N, T, X) was rapidly presented in the center of the gratings. The size of the letters was 0.25° .

Design and procedure

The purpose of the experiment was to test the extent to which the constriction of pupil size could be attributed to the attention that was captured by the presentation of gratings of different sizes. To this end, participants either performed an attention-demanding fixation task or simply passively viewed the stimulus during the recording of pupil size. To attract the participant's attention to the central fixation point, we used a rapid serial visual presentation (RSVP) paradigm, where participants were asked to report how many times the letter "X" (0, 1, 2, or 3) was presented in a series of red letters (Z, L, N, T, X) by pressing the corresponding number button. The presentation of the series of letters began 0.75 second before the onset of the grating stimuli and during the entire time the grating stimulus was on the screen. Previous studies (Chen, Zhou, Yang, & Fang, 2010; Kikuchi, Sekine, & Nakamura, 2001) have shown that this is an effective way of directing a participant's attention toward a central fixation point and, as a consequence, reducing the participant's attention directed toward the gratings. In the passive viewing condition, participants simply watched the presentation and did not perform any task. Please note that in the passive viewing session exactly the same stimuli were used (i.e., both gratings and letters were presented) to make sure that any difference between the passive-viewing session and the fixation-task session could not be attributed to the difference in stimuli. The absolute pupil sizes in the RSVP and passive-viewing tasks were significantly different (see Results section), confirming that our attention manipulation worked well.

The fixation task (i.e., the RSVP task) and the passive-viewing task were performed separately in different sessions. Each session (i.e., each task) consisted of eight runs with 12 trials per run (four trials for each of the three stimulus sizes). Six out of the 12 trials in each run included a target "X" in the series of letters, and the other six trials did not include the letter "X." In other words, in each run, there were two repetitions for each of the six conditions (3 sizes \times 2 with/without "X"). The order of sessions was randomized across participants.

Just as in the other two experiments, calibration and drifting corrections were carried out at the beginning of each run. Each trial was also triggered after participants maintained the fixation. In both sessions, a series of letters was presented in the center of the grating, with five of the letters being presented before the onset of the grating and 14 of them being presented together with the grating. Each letter was presented for 150 ms. In other words, the grating was presented from the 6th letter to the 19th letter, lasting 2.1 seconds. Pupil area was recorded right after the trigger key was pressed (Figure 3A). It took about 1 hour to finish this experiment.

Data analysis

The analysis was the same for all experiments. Trials with blinks or an eye position deviation of more than 1° from the central fixation point were excluded from the analysis (on average, 25% trials in Experiment 1, 25% trials in Experiment 2, and 16% trials in Experiment 3 were excluded). We then extracted the pupil area data from 0.5 second before the onset of the stimulus (i.e., grating; for Experiment 2, before the onset of the first grating) to the end of the stimulus presentation for each trial. The pupil area data were then converted to percentage change using the data before stimulus onset as the baseline. Note that, in Experiment 3, the baseline was the data 0.5 second before the onset of the grating; that is, there were also letters at the baseline stage just as there were during the grating presentation stage. This guaranteed that the percentage change in pupil area was induced by the onset of the grating, not the onset of the letters. Finally, the percentage change data were averaged across trials for each condition.

Repeated analyses of variance (ANOVAs) were done to reveal the main effect of size or task on the peak pupil constrictions. The Greenhouse–Geisser method was used to correct for violations of sphericity. Post hoc paired *t*-tests were performed to reveal any differences between conditions. To confirm these results, we also performed Bayesian statistics and report Bayes factors for each test with JASP 0.13 (<https://jasp-stats.org/>).

Results

Experiment 1: Pupil size increased with the size of gratings

Figure 2B shows the profile of pupillary responses to presentations of gratings of different sizes. The preliminary analysis showed that there was no significant difference between the pupil size induced by the two grating orientations; therefore, we collapsed the results of these two orientations. The profiles for the three grating size conditions look similar, in that the pupil area remained unaffected for about 300 ms (the onset of pupil constriction was 319 ms, 312 ms, and 308 ms for the 3°, 6°, and 9° gratings, respectively) (Bergamin & Kardon, 2003) and then began to decline. The constriction of pupil size reached its peak (i.e., the lowest value) at about 800 ms (801 ms, 743 ms, and 808 ms for the 3°, 6°, and 9° gratings, respectively) after the onset of the stimulus. After that, the pupil began to dilate and eventually reached the level of baseline.

The peak of pupil constriction for each participant is shown in Figure 2C, where each of the gray lines with symbols shows the results for each individual and the black line with symbols shows the results averaged across participants. The peak constriction was 6.94%, 10.88%, and 15.64% on average for the 3°, 6°, and 9° grating sizes, respectively. The main effect of grating size on pupil constriction was significant: Greenhouse–Geisser corrected $F(2, 10) = 11.00$, $p = 0.02$, and partial $\eta^2 = 0.69$. This result was confirmed by a Bayesian repeated-measures ANOVA (Bayes factor $[BF]_{10} = 18.77$), providing strong evidence for the main effect of grating size (Wagenmakers et al., 2018). The post hoc test showed that the pupil peak constriction for the 9° grating was significantly larger than it was for the 6° grating ($t = 3.36$, $p = 0.02$, $BF_{10} = 4.09$) or the 3° grating ($t = 3.40$, $p = 0.02$, $BF_{10} = 4.24$) and that the constriction for the 6° grating was significantly larger than it was for the 3° grating ($t = 2.92$, $p = 0.03$, $BF_{10} = 2.84$). These results suggest that, even when the mean luminance of the gratings of three sizes was matched, there was a significant effect of grating size on pupil constriction.

Linear summation is a rule at some level of basic response (Chen, Yu, Zhu, Peng, & Fang, 2016; Ferster & Jagadeesh, 1991; Magnussen & Kurtenbach, 1980; Tolhurst & Dean, 1990). For example, the amplitude of the first visual-evoked potential component, C1, follows a linear additive model for gratings of different sizes. In addition, a previous study (Wang, Boehnke, Itti, & Munoz, 2014) found that the pupil response to audiovisual stimuli can be predicted by the linear summation of the pupil response to each modality. Here, we also tested whether the pupil response to grating size follows the linear summation rule. The

dashed curve in Figure 2B shows the sum of the pupil response to 3° and 6° gratings, which looks similar to the pupil response to the 9° grating. We compared the peak constriction of the 9° grating with the sum of the peak constriction of the other two sizes. The peak constriction showed no significant difference ($t = 0.98$, $p = 0.37$, $BF_{10} = 0.54$).

One may argue that the effect of grating size on pupil constriction was not due to that visual feature but to variations in the amount of attention attracted by the small versus large gratings. We will discuss the contribution of attention in Experiments 2 and 3.

Experiment 2: Pupil size switched with the switch of grating size

In Experiment 2, we tested how pupil size changes with an increase or a decrease in grating size and whether or not the order of the presentation matters. In one condition, a grating of 3° was presented first, followed by a grating of 9° (“first small, then large”). In the other condition, the 9° grating was presented first followed by the 3° grating (“first large, then small”) (Figure 3A).

We found that, the pupil constriction changes rapidly with grating size (Figure 3B). In the “first small, then large” condition, pupils first constricted slightly to the 3° grating (peak constriction, 6.77%) and then constricted further after presentation of the 9° grating (peak constriction, 11.80%). The change in constriction was significant (peak constriction, paired t -test, $t = 6.58$, $p < 0.001$) (Figure 3C). Bayesian paired t -tests indicated strong evidence of modulation of grating size on pupil constriction ($BF_{10} = 31.85$). In the “first large, then small” condition, pupils constricted quite a bit at first (12.86%), and then the constriction became smaller (7.93%) after presentation of the second stimulus (paired t -test, $t = 6.51$, $p < 0.001$, $BF_{10} = 23.01$) (Figure 3C).

Regardless of the presentation order, pupil constriction to the small grating was roughly the same ($t = 0.60$, $p = 0.58$; $BF_{10} = 0.41$), as was constriction to the large grating ($t = 0.59$, $p = 0.58$, $BF_{10} = 0.40$). This suggests that the amount of pupil constriction corresponded steadily to the visual feature (i.e., size) of the gratings. Indeed, if the pupil constriction was a result of the amount of attention attracted by the gratings, then it would be unlikely that the pupil constriction would remain the same independent of the order in which the grating was presented. In other words, bottom-up attention to the same grating should be not as strong when it was presented first as when it was presented second—and this was clearly not the case. We will further investigate the role attention in Experiment 3.

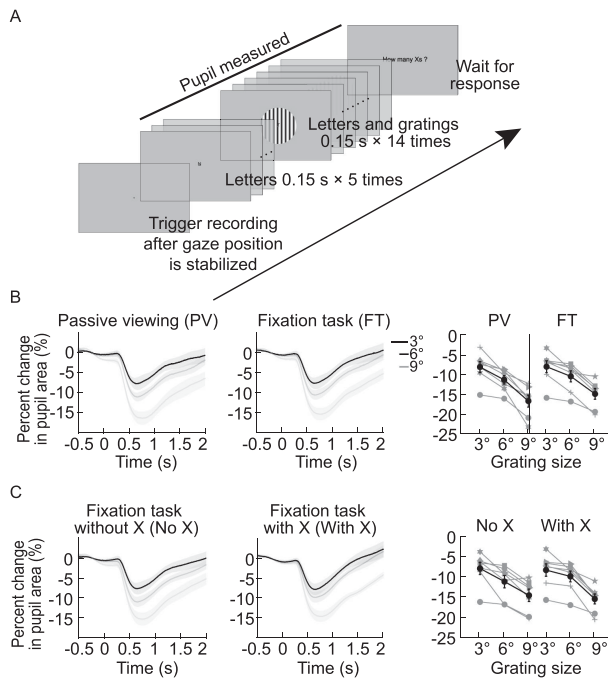


Figure 4. Stimuli, protocol, and results of Experiment 3. (A) A series of letters was presented rapidly (each for 0.15 second) before and during presentation of the grating stimulus. In the passive-viewing session, participants were asked to passively view the stimulus. In the fixation-task session, participants were asked to report how many letters “X” were presented by pressing a corresponding button (0, 1, 2, or 3). (B) The profile of percent change in pupil area in each session (left and middle panels) and the peak constrictions (right panel) when participant were performing the passive-viewing task or the fixation-task. (C) The profile of percent change in pupil area in each session (left and middle panels) and the peak constrictions (right panel) in trials without the letter “X” or with at least one letter “X” when participants were performing the fixation task.

Experiment 3: Attention is not critical for the modulation of grating size on pupil size

In two separate sessions, participants were asked either to view the grating stimuli passively or to report how many times the letter “X” was presented in a series of rapidly presented letters (RSVP task) in the center of the grating stimulus (Figure 4A). Here, five letters were presented (each for 0.15 second) before the onset of the grating and another 14 letters were presented during the entire time the grating was on the screen, which meant that a participant’s attention was attracted to the center of the screen 0.75 second before stimulus onset and remained there during the entire time the grating was present. In this case, participants paid little (if any) attention to the grating stimulus. As a result, by comparing the pupillary response when participants were performing the RSVP task with when they were

performing no task (i.e., passively viewing), we expected to reveal the contribution of attention (if any) to the effect of grating size on the pupillary response.

Our own earlier study (Chen et al., 2010) showed that this manipulation works. In that study, we found that an effect that was observed in passive viewing disappeared in the central RSVP condition. Moreover, the absolute pupil size before the grating stimulus was presented differed significantly between the RSVP and passive-viewing tasks [main effect of attention, $F(1, 6) = 5.11$, $p = 0.065$, $BF_{10} = 528.60$], suggesting again that our manipulation of attention worked well.

In the RSVP task, the response accuracy was 83.68%. The profiles of pupil size in all conditions are shown in Figure 4B. A repeated-measures ANOVA was performed to reveal the main effect of size and attention on the peak of the pupil constriction and the interaction of these two factors. We found a significant main effect of grating size [Greenhouse–Geisser corrected, $F(2, 12) = 52.53$, $p < 0.001$, partial $\eta^2 = 0.90$], but the main effect of attention [$F(1, 6) = 0.37$, $p = 0.57$] and the interaction between attention and grating size [$F(2, 12) = 1.76$, $p = 0.21$] was not significant. These results were confirmed by a Bayesian repeated-measures ANOVA, providing strong evidence for the main effect of grating size ($BF_{10} = 8.17 \times 10^5$) but little evidence for the effect of attention ($BF_{10} = 0.37$) or for the interaction effect ($BF_{10} = 0.31$).

In the fixation-task session, there were trials with at least one letter “X” and trials without the letter “X.” It is possible that the presentation of the target “X” may have contributed to the pupillary response and somehow affected the final results. To rule out this possibility, we divided the trials in the fixation task into two groups according to the presence of the letter “X.” We found that the main effect of the presence of the letter “X” on pupil size was not significant [$F(1, 6) = 0.001$, $p = 0.98$, $BF_{10} = 0.30$].

Discussion

Here we provide converging evidence that, even when the mean luminance of stimuli is kept constant, features such as the size of the stimulus can influence pupil constriction. In addition, this influence is steady and robust with little or no influence of stimulus order and attention. Because the change in grating size is essentially a change in the spatial structure of the stimulus when the mean luminance is matched to the luminance of the background, our finding is consistent with previous findings that the spatial structure, color, and movement modulate pupil size (Barbur, Harlow, & Sahraie, 1992; Ukai, 1985).

Previous studies have shown that covert attention influences pupil response (Binda & Gamlin, 2017; Binda et al., 2013a; Binda et al., 2014; Gabay et al., 2011;

Kang et al., 2014; Wierda et al., 2012; Willems et al., 2014). However, we did not observe a significant effect of attention. It is possible that the effect of size in our study is strong enough to be immune to any influence of the lack of attention. Indeed, our stimuli were presented in fovea, which induces much larger pupil constriction than that observed in studies where the stimuli were presented in the visual periphery (Binda et al., 2013a; Binda et al., 2014). Although the significantly different pupil size before grating presentation suggests that our control of attention was effective, it is still possible that it was not strict enough because each participant's attention was still deployed at the central visual field in the RSVP task. An even stricter control of attention is necessary to further examine how attention might modulate pupil constriction induced by grating size.

Why would the size of gratings of equal-luminance modulate pupil constriction? One possibility is that the function of luminance on pupil response is not linear (Barbur & Thomson, 1987), and pupil constriction is more affected by bright than dark stripes of the gratings. As a result, even when the mean luminance is constant the overall bright area increases with the size of grating, which makes the pupil constriction also increase; however, this does not explain why pupil constriction is modulated by the spatial frequency of a grating. Because the influence of spatial frequency on pupil constriction is very similar to the contrast sensitivity function, researchers have suggested that pupil constriction to visual stimuli also reflects visual processing in the cerebral cortex (Barbur & Thomson, 1987; Weiskrantz, Cowey, & Le Mare, 1998; Weiskrantz et al., 1999). If this is the case, then it is not surprising that pupil constriction increases with stimulus size. Direct evidence of this explanation, however, is still lacking.

Because visual features, including luminance, size, spatial frequency, eccentricity, color, and movement, all influence pupil size, one must be extremely cautious when testing the effect of various visual stimuli on pupil size. To be more specific, an inverted, phase- or spatially scrambled, or shrunken/expanded version of the original image may not provide good control conditions, because one or more other visual features will also be changed accordingly. One strategy to rule out the confound of these visual features is to focus on the interaction among factors instead of the direct contrast between two conditions (i.e., two groups of images) (Laeng & Sulutvedt, 2014).

Conclusions

Overall, our finding suggests that a match of mean luminance does not guarantee equal pupillary responses.

Keywords: pupil size, grating size, luminance, attention

Acknowledgments

Supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (RGPIN-2017-04088 to MAG), a grant from the Canadian Institute for Advanced Research (to MAG), two grants from the National Natural Science Foundation of China (31800908 and 31970981 to JC), and a grant from the Key Realm R&D Program of Guangzhou (202007030005 to JC). JC, YY, and MAG designed the study; AK and JC performed the research; JG and JC analyzed the data; JG and JC wrote the manuscript; and JC, AK, YY, and MAG revised the manuscript.

Commercial relationships: none.

Corresponding author: Juan Chen.

Email: juanchen@m.scnu.edu.cn.

Address: Key Laboratory of Brain, Cognition and Education Sciences, Ministry of Education; Center for the Study of Applied Psychology; Guangdong Key Laboratory of Mental Health and Cognitive Science, School of Psychology, South China Normal University, Guangzhou, Guangdong Province, China.

References

- Barbur, J., Harlow, A., & Sahraie, A. (1992). Pupillary responses to stimulus structure, colour and movement. *Ophthalmic and Physiological Optics*, *12*(2), 137–141.
- Barbur, J., & Thomson, W. D. (1987). Pupil response as an objective measure of visual acuity. *Ophthalmic and Physiological Optics*, *7*(4), 425–429.
- Bergamin, O., & Kardon, R. H. (2003). Latency of the pupil light reflex: Sample rate, stimulus intensity, and variation in normal subjects. *Investigative Ophthalmology & Visual Science*, *44*(4), 1546–1554, <https://doi.org/10.1167/iovs.02-0468>.
- Binda, P., & Gamlin, P. D. (2017). Renewed attention on the pupil light reflex. *Trends in Neurosciences*, *40*(8), 455–457.
- Binda, P., Pereverzeva, M., & Murray, S. O. (2013a). Attention to bright surfaces enhances the pupillary light reflex. *Journal of Neuroscience*, *33*(5), 2199–2204.
- Binda, P., Pereverzeva, M., & Murray, S. O. (2013b). Pupil constrictions to photographs of the sun. *Journal of Vision*, *13*(6):8, 1–9, <https://doi.org/10.1167/13.6.8>.

- Binda, P., Pereverzeva, M., & Murray, S. O. (2014). Pupil size reflects the focus of feature-based attention. *Journal of Neurophysiology*, *112*(12), 3046–3052.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Chen, J., Yu, Q., Zhu, Z., Peng, Y., & Fang, F. (2016). Spatial summation revealed in the earliest visual evoked component C1 and the effect of attention on its linearity. *Journal of Neurophysiology*, *115*(1), 500–509.
- Chen, J., Zhou, T., Yang, H., & Fang, F. (2010). Cortical dynamics underlying face completion in human visual system. *The Journal of Neuroscience*, *30*(49), 16692–16698.
- Einhäuser, W., Stout, J., Koch, C., & Carter, O. (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proceedings of the National Academy of Sciences, USA*, *105*(5), 1704–1709.
- Ferster, D., & Jagadeesh, B. (1991). Nonlinearity of spatial summation in simple cells of areas 17 and 18 of cat visual cortex. *Journal of Neurophysiology*, *66*(5), 1667–1679.
- Gabay, S., Pertzov, Y., & Henik, A. (2011). Orienting of attention, pupil size, and the norepinephrine system. *Attention, Perception, & Psychophysics*, *73*(1), 123–129.
- Kang, O. E., Huffer, K. E., & Wheatley, T. P. (2014). Pupil dilation dynamics track attention to high-level information. *PLoS One*, *9*(8), e102463.
- Kikuchi, T., Sekine, M., & Nakamura, M. (2001). Functional visual field in a rapid serial visual presentation task. *Japanese Psychological Research*, *43*(1), 1–12.
- Laeng, B., & Endestad, T. (2012). Bright illusions reduce the eye's pupil. *Proceedings of the National Academy of Sciences, USA*, *109*(6), 2162–2167.
- Laeng, B., & Sulutvedt, U. (2014). The eye pupil adjusts to imaginary light. *Psychological Science*, *25*(1), 188–197.
- Magnussen, S., & Kurtenbach, W. (1980). Linear summation of tilt illusion and tilt aftereffect. *Vision Research*, *20*(1), 39–42.
- Naber, M., & Nakayama, K. (2013). Pupil responses to high-level image content. *Journal of Vision*, *13*(6):7, 1–8, <https://doi.org/10.1167/13.6.7>.
- Partala, T., & Surakka, V. (2003). Pupil size variation as an indication of affective processing. *International Journal of Human-Computer Studies*, *59*(1–2), 185–198.
- Sahraie, A., Trevethan, C. T., MacLeod, M. J., Urquhart, J., & Weiskrantz, L. (2013). Pupil response as a predictor of blindsight in hemianopia. *Proceedings of the National Academy of Sciences, USA*, *110*(45), 18333–18338.
- Slooter, J., & van Norren, D. (1980). Visual acuity measured with pupil responses to checkerboard stimuli. *Investigative Ophthalmology & Visual Science*, *19*(1), 105–108.
- Sperandio, I., Bond, N., & Binda, P. (2018). Pupil size as a gateway into conscious interpretation of brightness. *Frontiers in Neurology*, *9*, 1070.
- Sterpenich, V., D'Argembeau, A., Desseilles, M., Baeteau, E., Albouy, G., Vandewalle, G., . . . Maquet, P. (2006). The locus ceruleus is involved in the successful retrieval of emotional memories in humans. *The Journal of Neuroscience*, *26*(28), 7416–7423.
- Stoll, J., Chatelle, C., Carter, O., Koch, C., Laureys, S., & Einhäuser, W. (2013). Pupil responses allow communication in locked-in syndrome patients. *Current Biology*, *23*(15), R647–R648.
- Tolhurst, D. J., & Dean, A. F. (1990). The effects of contrast on the linearity of spatial summation of simple cells in the cat's striate cortex. *Experimental Brain Research*, *79*(3), 582–588.
- Ukai, K. (1985). Spatial pattern as a stimulus to the pupillary system. *Journal of the Optical Society of America A*, *2*(7), 1094–1100.
- Wagenmakers, E.-J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., . . . Morey, R. D. (2018). Bayesian inference for psychology. Part II: Example applications with JASP. *Psychonomic Bulletin & Review*, *25*(1), 58–76.
- Wang, C.-A., Boehnke, S. E., Itti, L., & Munoz, D. P. (2014). Transient pupil response is modulated by contrast-based saliency. *The Journal of Neuroscience*, *34*(2), 408–417.
- Weiskrantz, L., Cowey, A., & Barbur, J. (1999). Differential pupillary constriction and awareness in the absence of striate cortex. *Brain*, *122*, 1533–1538.
- Weiskrantz, L., Cowey, A., & Le Mare, C. (1998). Learning from the pupil: a spatial visual channel in the absence of V1 in monkey and human. *Brain*, *121*, 1065–1072.
- Wierda, S. M., van Rijn, H., Taatgen, N. A., & Martens, S. (2012). Pupil dilation deconvolution reveals the dynamics of attention at high temporal resolution. *Proceedings of the National Academy of Sciences, USA*, *109*(22), 8456–8460.
- Willems, C., Damsma, A., Wierda, S. M., Taatgen, N., & Martens, S. (2014). Training-induced changes in the dynamics of attention as reflected in pupil dilation. *Journal of Cognitive Neuroscience*, *27*(6), 1161–1171.