Pupil constrictions to photographs of the sun

Paola Binda
Department of Psychology, University of Washington, Seattle, WA, USA
Department of Physiological Sciences, Universita' di Pisa, Pisa, Italy

Maria Pereverzeva
Department of Psychology, University of Washington, Seattle, WA, USA

Scott O. Murray
Department of Psychology, University of Washington, Seattle, WA, USA

The pupil constricts in response to light increments and dilates with light decrements. Here we show that a picture of the sun, introducing a small overall decrease in light level across the field of view, results in a pupillary constriction. Thus, the pictorial representation of a high-luminance object (the sun) can override the normal pupillary dilation elicited by a light decrement. In a series of experiments that control for a variety of factors known to modulate pupil size, we show that the effect (a) does not depend on the retinal position of the images and (b) is modulated by attention. It has long been known that cognitive factors can affect pupil diameter by producing pupillary dilations. Our results indicate that high-level visual analysis (beyond the simple subcortical system mediating the pupillary response to light) can also induce pupillary constriction, with an effect size of about 0.1 mm.

Introduction

Light level is the primary determinant of pupil size. When ambient light is bright, the pupil constricts, resulting in a decrease in retinal illumination, and when ambient light is dim, the pupil dilates, resulting in an increase in retinal illumination. This modulation of pupil size affects visual signals in multiple ways. At very low light levels, dilated pupils increase the probability of photon capture by the retina, increasing sensitivity. At high light levels, pupil constriction reduces the level of light adaptation, thereby reducing the time required to restore sensitivity after an abrupt light decrement (Campbell & Woodhouse, 1975; Woodhouse & Campbell, 1975). In less extreme conditions, pupil size affects depth of field (Charman & Whitefoot, 1977; Marcos, Moreno, & Navarro, 1999) and acuity (Westheimer, 1964), with smaller pupils reducing optical aberrations and enhancing the optical quality of the retinal image (Campbell & Gregory, 1960; Woodhouse, 1975; Laughlin, 1992; Liang & Williams, 1997). The anatomical circuit mediating these basic light responses involves a direct projection from the retina to subcortical nuclei, which in turn control subcortical pupillomotor centers (Loewenfeld, 1993; Gamlin & Clarke, 1995).

An extensive literature reports that nonvisual factors such as arousal and memory load can induce pupillary dilation but do not produce pupillary constriction (Hess & Polt, 1960; Kahneman & Beatty, 1966; Einhauser, Stout, Koch, & Carter, 2008; Nassar et al., 2012; Wierda, van Rijn, Taatgen, & Martens, 2012). In addition, psychophysical and clinical evidence has suggested that the pupillary constriction in response to light may be affected by cortical visual processing (Lorber, Zuber, & Stark, 1965; Barbur, 2004). For example, pupillary constriction in response to a light increment is smaller when presented to the blind portion of the visual field of patients with a lesion in early visual cortex compared with the presentation in the intact visual field (Cibis, Campos, & Aulhorn, 1975; Kardon, 1992; Barbur, 2004). Here we ask whether pupil size depends on complex features of the visual stimulus, presumably processed in cortical areas. Specifically, we tested whether the pictorial representation of the sun in images such as Figure 1A would lead to a pupil constriction (relative to a series of control images), overriding the pupillary dilation that would normally occur in response to a light decrement (Experiment 1). In addition, we address the potential

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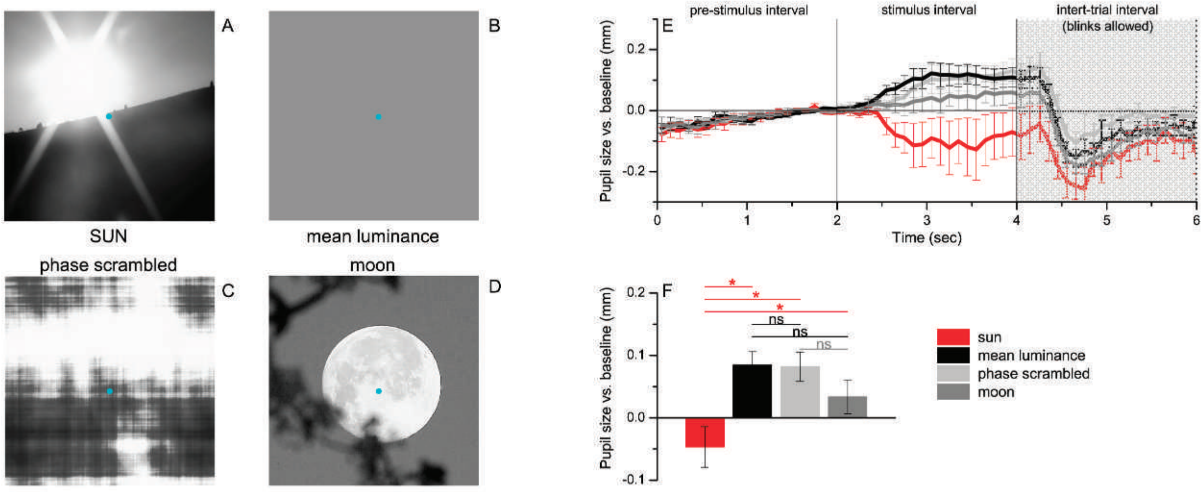

Figure 1. Pupillary responses to pictures of the sun and control images (Experiment 1). (A–D) Illustrative examples of the four categories of images. A and D are public domain images; the images actually used in the experiments are available at: http://faculty.washington.edu/ somurray/PupilSun/. (E) Baseline-corrected pupil size plotted as a function of time from trial onset (the baseline pupil diameter during the 500 ms preceding the stimulus presentation was subtracted from each trace, and these were averaged across subjects, $n = 8$). Vertical lines mark the stimulus presentation window; the gray-shaded area marks the intertrial interval. (F) Baseline-corrected pupil size during the stimulus interval, averaged across subjects. Error bars are *SEM* across subjects. Asterisks mark statistically significant pairwise comparisons across image categories (Tukey's HSD).

confound of differential spatial distribution of luminance across image categories by replicating the experiment at different retinal eccentricities (Experiment 2), and we measure the effect of task-related variables by manipulating the location of attention (Experiments 3–4).

Methods

Subjects and apparatus

Eight subjects (four females) with normal or corrected-to-normal vision (average age of 30 years) participated in Experiments 1, 3, and 4 (the three authors and five lab associates who were naïve to the aims of the study); seven of these (four naïves) participated in Experiment 2. Subjects gave written informed consent prior to their participation. Experimental procedures were approved by the University of Washington Human Subjects Institutional Review Board and were in line with the Declaration of Helsinki.

Stimuli were presented on a 35 × 28 cm CRT monitor, subtending 24° × 18° of visual angle at the viewing distance of 81 cm; a chin rest was used to stabilize head position. The experimental room had no illumination other than the display screen. Visual displays were generated in Matlab (Mathworks) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Stimuli

The stimuli consisted of 7° × 7° grayscale images, presented after a uniform white screen of maximum monitor luminance, 121 cd/m^2. There were four image categories: (a) photographs of the sun (Figure 1A); (b) uniform luminance squares that matched the mean luminance of each sun image (Figure 1B); (c) phase-scrambled images of the sun (Figure 1C) that preserved mean luminance, power spectrum, and root mean square contrast (Olman, Ugurbil, Schrater, & Kersten, 2004), and (d) photographs of the moon that were adjusted to match the mean luminance of the sun images (Figure 1D). Note that the images in Figure 1A through D are only illustrative examples; the images actually used in the experiments are available at http://faculty.washington.edu/somurray/PupilSun/. There were 13 images per category. Their mean luminance was matched across categories; within each category, mean luminance ranged between 22.6 and 60.1 cd/m^2 (values reported on the abscissa of Figure 3). However, the spatial distribution of luminance (quantified as the mean luminance in concentric disks of increasing radius) varied across categories; at the center of the image, luminance tended to be higher in the sun pictures than in all other image categories. Specifically,

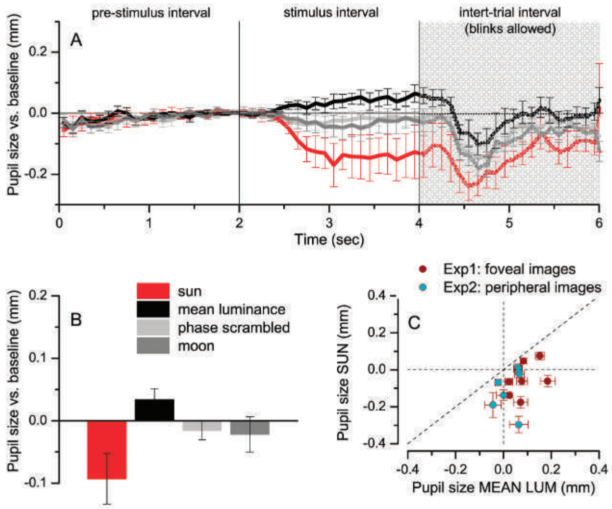

Figure 2. Pupillary responses to pictures presented in the periphery (Experiment 2). (A) Baseline-corrected pupil size traces ($n = 7$). (B) Baseline-corrected pupil size during the stimulus interval, averaged across subjects. Error bars are *SEM* across subjects. (C) Individual subjects data from Experiments 1 and 2: baseline-corrected pupil size during the stimulus interval, plotting data for the sun images against the mean-luminance images. Error bars are *SEM* across trials.

the average luminance in the central 1° of the sun pictures was significantly higher than in the same area of the mean luminance squares (two-sample t test, $p = 0.007$) but nonsignificantly different from the luminance in the central 1° of the phase-scrambled and moon pictures (all p values >0.08).

Procedure

One experimental run was composed of 52 trials, presenting the full set of images in random order. A fixation mark (a 0.2° cyan dot) was presented at the center of the screen and was always visible. Trials started with a 2-s blank prestimulus epoch in which subjects fixated the maximum luminance screen (121 cd/m^2). This was followed by a 2-s stimulus epoch in which one of the images was displayed (the area of the screen outside the image was constant at all times and equal to 121 cd/m^2), reducing the overall luminance level across the screen by 8 cd/m^2 on average. For Experiments 1, 3, and 4, the images were presented at screen center (i.e., centered at fixation); for Experiment 2, they were presented 10° to the right of fixation. Subjects were asked to refrain from blinking during the prestimulus and stimulus epochs. The extinction of the image marked the end of a trial. In the 2-s intertrial interval that followed, subjects were allowed to blink, and they were asked to press one of three designated keys (depending on the behavioral task).

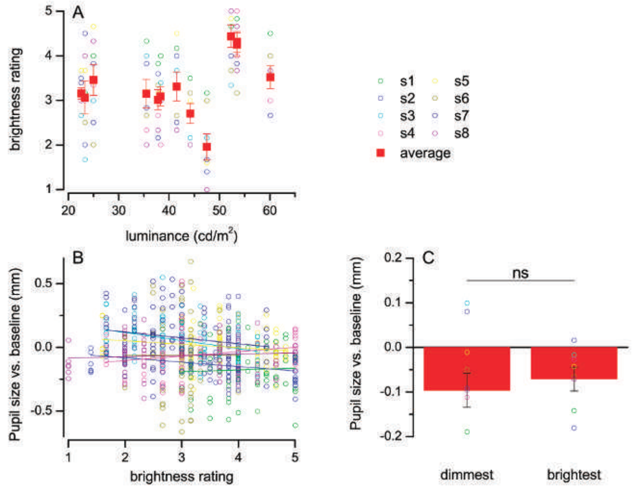

Figure 3. Relationship between pupil size and brightness of the sun images. (A) Brightness ratings versus luminance for the 13 sun images; across subjects, ratings were significantly correlated with luminance (mean correlation: 0.33 ± 0.11; one-sample t test: $t = 3.20$, $p = 0.015$). Error bars are *SEM* across subjects. (B) Average pupil size during the presentation of the sun images in Experiment 1 is plotted (across all trials and for all subjects) against the brightness of each image; linear regressions are shown. (C) Pupil size during the presentation of sun images (Experiment 1) in the first and fourth quartiles of brightness rating (i.e., those rated as dimmest and brightest). Error bars are *SEM* across subjects; circles show data from the individual subjects.

In separate sessions, subjects performed different tasks. In the passive viewing condition (Experiments 1 and 2), subjects simply categorized the images by pressing one of three keys: (a) "photographs," which included sun and moon images; (b) equal-luminance squares; and (c) phase-scrambled images. In the central fixation task condition (Experiment 3), the 0.2° fixation mark underwent brief (100-ms) threshold-level color changes during the 2-s stimulus interval. Subjects were required to count the number (1–3) of changes and report it with a button press after the offset of the images. In the peripheral task condition (Experiment 4), the same task was performed on a 0.2° dot in the periphery, positioned 10° to the right of fixation (and therefore 10° away from the center of the images). Task difficulty (the magnitude of color changes) was adjusted to maintain performance at about the 70% level.

Brightness ratings

Brightness ratings for the sun images were collected from all subjects, in a separate session. This was composed of two runs, with each of the 13 sun images presented three times in random order (yielding a total of six brightness ratings per image and subject). As in Experiment 1, the images were presented for 2 s following a uniform white screen of maximum luminance; subjects maintained fixation at the center of the image. Upon image extinction, subjects had an unlimited time to rate the image brightness on a 1 to 5 scale, and a new image was presented 500 ms after the response was recorded; no eye-tracking data were collected.

Eye tracking

Pupil diameter and two-dimensional eye position were measured monocularly with a video-based eye tracker (ASL Eyetrack 6, remote sensor mounted below the monitor screen). A standard nine-point calibration was run at the beginning of each session. Eye-tracking data were acquired at 120 Hz. Time-points with unrealistic pupil size (<2 mm or >8mm) or eye position (locations outside the screen monitor) were treated as signal losses. Eye-position samples were tightly clustered around the fixation point (the difference between the 5th and the 95th percentile of eye position samples during the stimulus interval was below 2°, similar across image categories and experiments), indicating that subjects accurately maintained fixation.

The baseline pupil diameter during the 500 ms preceding the stimulus presentation was subtracted from each individual trace. Across subjects, the average pupil size while viewing the blank screen was 3.76 mm ($SD = 0.55$ mm), roughly consistent with the 3.53 mm predicted by Watson and Yellott's (2012) unified formula—the formula assumes a homogeneous field with circular shape; in our case, the field was rectangular with an area equivalent to a circle of 23.45° diameter (luminance of the field: 121 cd/m^2; average age of subjects: 30 years). Baseline-corrected data were averaged in 100-ms temporal bins to yield the pupil size time courses (e.g., Figure 1E) or during the 2-s stimulus interval for comparison across conditions (e.g., Figure 1F; averaging data over smaller temporal windows did not qualitatively alter the results). Data from the intertrial interval were never included in statistical analyses, being likely contaminated by blinks (which were strongly discouraged during the prestimulus and stimulus interval). For all experiments, analyses included a minimum of six runs per subject (312 trials per experiment and subject).

Statistical analyses

All statistical analyses took a repeated-measures approach, comparing pupil size averages in the stimulus presentation interval (2–4 second into the trial). For Experiment 1, we evaluated the significance all six pairwise comparisons across image categories; to account for the increased risk of Type I error due to multiple comparisons, statistical significance was assessed using the Tukey's Honestly Significant Difference (HSD) criterion. A paired two-sample t test was employed to compare pupil size measurements across subsamples of images (Figure 3C). Across experiments, the effects of image category, eccentricity, and attention were evaluated with two-way repeated-measure analyses of variance (ANOVAs). Correlations (between brightness ratings and luminance or between pupil size measurements in the stimulus interval and luminance/brightness) were assessed in each subject; the distribution of correlation values across subjects was then evaluated against the null hypothesis of a 0 correlation with a one-sample t test.

Results

We measured pupil size changes in response to the presentation of images of the sun and three types of control images, all matched in average luminance (illustrative examples in Figure 1A through D). Figure 1E shows the time course of pupil size (averaged across the eight subjects) for each image category, and Figure 1F shows the average pupil diameter during the 2-s stimulus presentation interval. All images were presented after a uniform white screen of maximum luminance (the luminance outside the images was constant at all times and equal to the maximum monitor luminance), thereby reducing the overall luminance level across the screen area. For the uniform squares, the phase-scrambled and the moon images, the stimulus presentation induced a small pupillary dilation (detailed in the next paragraph). However, this was not the case for the sun images. A series of statistical tests comparing pupil size across the four image categories (corrected for multiple comparisons) confirms that pupil size is significantly different for the sun images than for the other three image categories (asterisks in Figure 1F), whereas there are no significant differences among the other image categories. Note that a pronounced pupillary constriction follows the offset of the image, possibly caused by the consequent increment of overall luminance across the screen. However, the interpretation of recordings from the intertrial interval (the beginning of which was marked by the image offset) are complicated by the presence of motor responses (the key press required by the task) and blinks (which were only allowed during this interval), both known to affect pupil size (Hupe, Lamirel, & Lorenceau, 2009).

The approximate amount of pupillary dilation expected from the presentation of the images can be predicted from Watson and Yellott's (2012) unified formula, given a rectangular field with area equivalent to a circle of 23.45° diameter, an overall luminance decrement across the field from 121 cd/m^2 to 113 cd/m^2, and an average age of the participants of 30 years. The dilation observed for the mean luminance and phase-scrambled pictures (about 0.1 mm) is larger than predicted by the formula (0.03 mm); however, the computations assume a homogeneous luminance distribution (whereas the image presentation changed luminance in a small portion of the field) with no effect of eccentricity (the importance of which is described in the next section), clearly an idealization in this case.

Although mean luminance was strictly matched across image categories, its spatial distribution was variable, and luminance at the center of the sun images tended to be higher than in the other image categories. Because pupillary responses are more sensitive to luminance changes occurring in the fovea (Clarke, Zhang, & Gamlin, 2003a), one might hypothesize that this small luminance difference explains the observed pupil size differences; note that this is unlikely, given the small size of our images (7° × 7°) and the large, bilateral receptive field sizes of the brainstem neurons (the Olivary nucleus of the pretectum) driving pupillary constrictions in response to luminance increments (Clarke, Zhang, & Gamlin, 2003b). This hypothesis predicts that the difference in pupil size between the sun and the other images should disappear when images are presented in the periphery of the visual field. Experiment 2, in which images were presented at 10° eccentricity, showed that this is not the case (Figure 2). Results from Experiments 1 and 2 were analyzed by means of a two-way repeated-measures ANOVA with factors image category (four levels) and image eccentricity (two levels). This shows significant main effects of image category ($F = 12.05$, $df = 3$, $p < 0.001$) and image eccentricity ($F = 9.77$, $df = 1$, $p = 0.02$) but no interaction between the two factors ($F = 2.10$, $df = 3$, $p = 0.13$). The main effect of eccentricity may be appreciated by comparing Figures 1 and 2. Across image categories, pupil size is smaller in Experiment 2, consistent with a reduced pupillary dilation when image presentation (and the consequent luminance decrement) occurs at a more peripheral location (Clarke et al., 2003a). Figure 2C plots pupil size for the sun images against pupil size for the mean-luminance square images for both Experiment 2 and Experiment 1. All points lay below the $x = y$ line, indicating that—at the single-subject level—pictures of the sun induced a pupillary constriction compared with luminance-matched uniform squares. Data points cluster in the lower-right quadrant of the axis, indicating that in the majority of subjects, pupillary constriction occurred in response to the sun images and pupillary dilation occurred in response to the luminance-matched squares. Observations from Experiments 1 and 2 lay at approximately the same distance from the $y = x$ line, representing the absence of a significant interaction between the factors of image category and eccentricity and implying that the effect of image category is the same irrespective of the retinal position of the images.

Note that the variability across subjects for the sun images is larger than for the other image categories (larger error bars in Figures 1E and 2A and more scattered points in Figure 2C for the sun images than for the mean luminance images), indicating that the pupillary response to the sun images is less consistent across subjects than the pupillary dilation in response to a luminance decrement. This can be expected if, as we hypothesize, the pupillary response to the sun images relies on mechanisms more complex than the simple subcortical circuit that is mainly responsible for the pupillary responses to luminance changes.

It has recently been suggested that brightness illusions can influence pupil size (Laeng & Endestad, 2012). Subjective brightness might vary across image categories. However, if brightness alone were responsible for the observed variations of pupillary responses, variations of brightness *within* image categories should result in differential pupillary constriction. To test this prediction, we asked subjects to rate the brightness of each sun image on a 1 to 5 scale (Figure 3A) and examined the relationship between brightness ratings and pupil size during the central presentation of the sun images (Experiment 1). Although pupil size is mildly correlated to the actual luminance of the sun images (mean correlation: -0.08 ± 0.03; $t = -2.67$, $p = 0.03$), there is no significant correlation between pupil size and brightness ratings (mean correlation: 0.08 ± 0.08; $t = -1.20$, $p = 0.27$, Figure 2B). In addition, pupil size during the presentation of the perceptually brightest and dimmest images (first and fourth quartiles of the brightness ratings distribution) are statistically indistinguishable (paired t test, $t = 0.80$, $p = 0.45$; Figure 2C).

We have recently shown that the distribution of attention strongly affects pupil size, such that attending to a brighter versus a darker region of the visual scene (without changing gaze position) results in a pupillary constriction (Binda, Pereverzeva, & Murray, 2013). In the first two experiments, the direction of attention was not tightly controlled (subjects categorized the images as photographs, uniform squares, and phase-scrambled images, an easy task we refer to as "passive fixation"). Therefore, attention might have been differentially distributed across image categories, focused on the brighter regions of the sun pictures and distributed more evenly in the other images, possibly explaining the pupillary constriction. To address this possibility, we performed two additional experiments designed to control the spatial distribution of attention. Attention was either focused at fixation, which corresponds to the center of the images (central fixation task, Experiment 3) or in the periphery (10° right of the center of the image, peripheral task, Experiment 4) to perform a challenging color change task—the proportion of correct responses was similar in the fixation task and peripheral task (0.78 ± 0.04 and 0.60 ± 0.08, respectively, one-way repeated-measures ANOVA, $F = 4.29$, $df = 1$, $p = 0.0769$).

Pupil size measurements in Experiments 3 and 4 are shown in Figure 4 and were analyzed using a two-way repeated-measures ANOVA with factors image category (four levels) and location of attention (two levels). Again, there is a main effect of image category ($F = 13.67$, $df = 3$, $p < 0.0001$). Moreover, for all image categories, there is a progressive dilation in the stimulus interval, during which the challenging task unfolded, and this is more pronounced with attention focused in the periphery (main effect of the location of attention: $F = 28.63$, $df = 1$, $p = 0.001$). The interaction between image category and direction of attention is nonsignificant ($F = 0.92$, $df = 3$, $p = 0.45$), indicating that the spatial distribution of attention did not affect the pupillary response to the sun pictures relative to the other images; this is also suggested by the time courses of pupil size for the four image categories, which run approximately parallel during the stimulus interval; note that the progressive increase of pupil size during the task interval is consistent with the well-known effect of increased pupil size with cognitive load (see the Discussion section).

It remains possible that the pupillary response to the sun images is affected by *what* is at the focus of attention: the images themselves, as in Experiment 1, versus a dot centered within or away from the images, as in Experiments 3 and 4. This is consistent with the results of an additional two-way ANOVA considering Experiments 1, 3, and 4 together and revealing a significant interaction between image category and a factor attention with three levels: attention to the images, to a dot centered within the images, or to a dot centered away from the images (main effect of image category: $F = 15.78$, $df = 3$, $p < 0.0001$; main effect of attention: $F = 13.42$, $df = 2$, $p < 0.001$; interaction: $F = 2.78$, $df = 6$, $p = 0.02$).

In summary, we have shown that the presentation of pictures of the sun induces a reduction in pupil size relative to control images of equal luminance. The effect cannot be explained by differences in the luminance distribution across image categories, pupil size does not relate to subjective impressions of brightness of the sun images, and the differential pupillary response across image categories is independent of the spatial distribution of attention but does depend on the task relevance of the images.

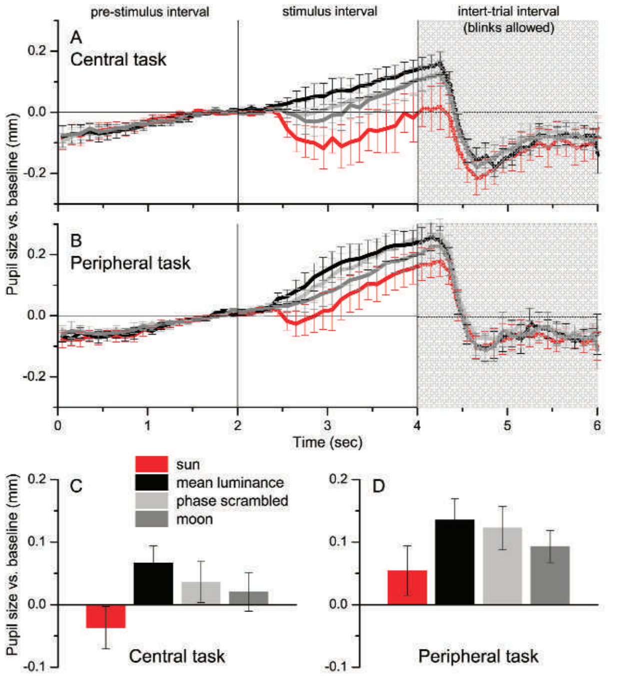

Figure 4. Pupillary responses to unattended pictures (Experiments 3 and 4). (A, B) Baseline-corrected pupil size traces ($n = 8$). (B, C) Baseline-corrected pupil size during the stimulus interval, averaged across subjects. Error bars are *SEM* across subjects.

Discussion

We presented pictures of natural scenes including the sun and the moon and control images of matched luminance. Because they appeared after a maximum-luminance computer monitor, all images equally reduced overall luminance. A simple model in which pupil size exclusively depends on luminance would therefore predict pupillary dilation for all image categories. However, we found that the sun pictures elicited pupillary constriction relative to the control images. The effect size is about 0.1 mm, which is small compared with the full range of pupil variation in humans (about 6 mm, i.e., between approximately 2 and 8 mm) but in the same order of magnitude as the pupillary response expected for the luminance change produced by the stimuli (a dilation of 0.03 mm is predicted by the unified formula in Watson & Yellott, 2012) and other known pupillary responses (given below). The effect was the same when the images were presented in central view or peripherally (Experiments 1 vs. 2), a finding that excludes the possibility that differences in the spatial distribution of luminance across image categories explains the effect.

A more sophisticated and accurate model of pupil behavior would incorporate contrast-dependent pupillary constrictions, that is, a transient reduction in pupil size evoked by the onset of visual stimuli, irrespective of their luminance (Clynes, 1961; Barbur, Harlow, & Sahraie, 1992; Young, Han, & Wu, 1993; Young & Kennish, 1993; Sahraie & Barbur, 1997; Barbur, 2004); these transient responses are about 0.05 to 0.2 mm. Still, this transient effect cannot account for our observation of a constriction in response to the sun pictures, sustained across the stimulus interval (see Figure 1E and 2A) and revealed by the comparison with control images matched in contrast (phase-scrambled images) and complexity (moon pictures). In addition, our analysis of subjective brightness ratings suggests that the pupillary response to the sun images is independent of its perceived light level, recently suggested to have a modulatory effect on pupil size (Laeng & Endestad, 2012). This finding is consistent with a recent demonstration that even cartoon depictions of the sun, which appear no brighter than cartoon depictions of the moon, can result in pupil constrictions (M. Naber and K. Nakayama, personal communication).

Pupil size is known to be modulated by cognitive factors, such as cognitive effort or "amount of attention" and decision making (Hess & Polt, 1960; Kahneman & Beatty, 1966; Einhauser et al., 2008; Nassar et al., 2012; Wierda et al., 2012), by changes in the focal distance (Marg & Morgan, 1949; Phillips, Winn, & Gilmartin, 1992; Bharadwaj, Wang, & Candy, 2011), as well as by the luminance of attended surfaces (Binda et al., 2013). Specifically, pupillary dilation is associated with increased cognitive effort. Note that this explains the progressive pupillary dilation found in Experiments 3 and 4 (Figure 4); pupillary constriction accompanies decreases in the focal distance, and a pupillary constriction results from paying attention to a more versus less luminous surface. The size of these three effects is generally less than 1 mm. It is possible that when subjects passively viewed the images, their attention was focused on the higher luminance regions of the sun pictures and more evenly distributed for the other image categories; it is also possible, albeit unlikely, that passive viewing of the sun pictures induced a decrease of the focal distance. Perhaps even more unlikely, reduced cognitive-related dilation during the presentation of sun pictures might ensue if subjects had less difficulty in categorizing the sun pictures relative to the control images—the simple task performed in Experiments 1 and 2.

However, these factors cannot explain our observation of differential pupillary responses across image categories when subjects were engaged in a demanding task (detecting color changes on the fixation spot or a peripheral target, Experiments 3 and 4), which maintained the location of spatial attention constant across image categories, required subjects to keep the stimulus plane in sharp focus, and involved an approximately constant level of cognitive effort.

Having controlled for these factors, and given that the differential pupillary responses to the sun and the control images did not depend on the retinal position of the images (Experiment 1 vs. 2) but did depend on their task relevance (comparison across Experiments 1, 3, and 4), we suggest that the observed effect is related to the processing of complex information, beyond the simple retinal and subcortical processing that is principally responsible for the pupillary response to luminance (Loewenfeld, 1993). Multiple complex features distinguish the pictures of the sun from the control images, and the processing of these features likely depends on attention to the image (Fang, Boyaci, Kersten, & Murray, 2008). For example, the luminance gradient profile is a characteristic feature of images depicting luminance sources and self-luminant objects (Zavagno & Caputo, 2001). A major distinctive feature of the sun images is, of course, their abstract content: whether or not they depict a sun. It is possible that the pupillary response to the sun pictures results from a conditioned light-avoidance behavior, that is, a pupil size change in the same direction as would be induced by the powerful irradiance of the sun, but note that previous attempts to obtain pupillary constriction from conditioned association of neutral and high-luminance stimuli have reportedly failed (Loewenfeld, 1993).

Although we can only speculate on the causes of the pupillary response to the sun images, our results clearly indicate that high-level factors can induce pupillary constriction, in addition to well-known pupillary dilations (e.g., the effect of cognitive load discussed above). In particular, our results are consistent with previous data suggesting that pupillary responses to luminance are modulated by input from the geniculo-cortical visual pathways (Cibis et al., 1975; Kardon, 1992; Barbur, 2004). Reduced pupillary responses are observed when stimulus visibility is impaired due to binocular rivalry or saccadic eye movements (Lorber et al., 1965; Richards, 1966; Zuber, Stark, & Lorber, 1966), and pupil size depends on the luminance of an attended surface (Binda et al., 2013). Together with our current findings, this evidence suggests that high-level visual processes modulate one of the most basic physiological responses: the change in pupil size in response to light increments or decrements.

Keywords: pupillary light reflex, contextual effects, attention

Supplementary information

Please find the full set of images used for the experiments at this link: http://faculty.washington.edu/somurray/PupilSun/.

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Corresponding author: Paola Binda.
Email: p.binda1@in.cnr.it.
Address: University of Washington, Department of Psychology, Seattle, WA, USA.
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