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Abstract

If a mental image is a rerepresentation of a perception, then properties such as luminance or brightness should also be conjured up in the image. We monitored pupil diameters with an infrared eye tracker while participants first saw and then generated mental images of shapes that varied in luminance or complexity, while looking at an empty gray background. Participants also imagined familiar scenarios (e.g., a "sunny sky" or a "dark room") while looking at the same neutral screen. In all experiments, participants' eye pupils dilated or constricted, respectively, in response to dark and bright imagined objects and scenarios. Shape complexity increased mental effort and pupillary sizes independently of shapes' luminance. Because the participants were unable to voluntarily constrict their eyes' pupils, the observed pupillary adjustments to imaginary light present a strong case for accounts of mental imagery as a process based on brain states similar to those that arise during perception.

Keywords
pupillometry, imagery, perception, vision, attention

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"Is the brightness of a mental image comparable to that of the actual scene?" This question was first asked 130 years ago by Sir Francis Galton (1883/1907) in his famous "breakfast-table questionnaire" in which he asked acquaintances to "think of some definite object—suppose it is your breakfast table as you sat down to it this morning—and consider carefully the picture that rises before your mind's eye" (p. 58). The most common report about the "illumination" of the imagined breakfast items was a form of "mental vision." Galton's question points to the core of mental imagery's nature, in that it attempts to reveal the existence of a mental representation that preserves the perceptible qualities of a previously experienced stimulus and that is "visual" despite the absence of an external stimulation. Today's accounts of imagery do not rely on introspective reports anymore, but they still support the view that a mental image is a willed simulation of perception (Edelman, 2004; Moulton & Kosslyn, 2009). Nevertheless, a debate goes on about the extent to which mental imagery is based on "pictorial" or perceptible low-level features or can be identified with higher-level symbolic phenomena (cf. Kosslyn, Thompson, & Ganis, 2006; Pearson, Clifford, & Tong, 2008).

In the study reported here, we considered that (a) people can call up mental images voluntarily but (b) they cannot directly control the size of their eye pupil at will (e.g., one cannot willingly constrict the pupil in the same way one can blink one's eyes). Hence, if we were able to measure comparable adjustments of the pupils to imagined scenarios and their corresponding perceptions, this would incontrovertibly reveal that mental images do preserve the sensory qualities of a previously experienced stimulus. In other words, the presence of spontaneous physiological adaptations of the ocular system would indicate that mental images must be based on a brain state similar to that which arises during visual perception. With use of modern infrared eye-tracking technology, it is now easy to provide an objective and precise answer to Galton's crucial query about mental imagery. Here, we show that the diameter of the eye pupil, which we measured while participants imagined stimuli of varying brightness, adjusts to imaginary light by constricting in response to relatively "bright" mental images and by dilating in response to relatively "dark" mental images.

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Experiment 1

On an LCD monitor, we showed 17 healthy adults (12 females, 5 males; mean age = 22.7 years, *SD* = 4.6) 22 pictures of equilateral triangles (half of them pointing up and half pointing down; see Fig. 1). Stimuli were created using PowerPoint software. Each triangle was 5 cm long on each side, corresponding to 4° of visual angle in size. Across trials, the internal area of the triangle changed luminance in 11 steps of 20 units, ranging from 20 to 220 units. The background's luminance was set at source to be 120 units in the HSL (hue, saturation, and luminance) scale. The participants' eye pupils were monitored using an infrared eye-tracking device (SensoMotoric Instruments, Teltow, Germany). Before each perceptual stimulus, a baseline picture was presented for 1,000 ms. Each triangle was shown for 5 s, centered over the gray background. Next, a completely dark screen was shown for 8 s (i.e., a sufficient time for the pupil diameters to dilate toward baseline levels and let the afterimage of the form fade completely), after which participants saw just the gray background for 5 s while they imagined the previously seen triangle.

Measurements of luminance were taken from the screen with a Spyder 4 Elite photometer (Datacolor Imaging Solutions, Lawrenceville, NJ), which indicated that the background's luminance (as well as that of the baseline and imagery screens) corresponded to 21.7 cd/m^2, whereas the luminance of the surface of the brightest triangle was 78.5 cd/m^2 and that of the darkest was 0.9 cd/m^2. The luminance of the dark intermediate screen was 22.3 cd/m^2. Stimuli were shown in a pseudorandom order, which was fixed for all participants.

The diameter of participants' eye pupils not only systematically decreased during perception with increasing levels of luminance but also systematically decreased when participants were simply asked to imagine the previously seen triangle despite looking at an empty screen (Fig. 2). We subtracted pupil diameter during presentation of the baseline screen from that during presentation of the subsequent perception and imagery screens to calculate baseline-corrected pupillary changes (expressed in pixels) for each condition.

A repeated-measures analysis of variance (ANOVA) on these pupillary changes revealed highly significant effects of luminance, $F(10, 160) = 8.05$, $p < .0001$. Correlation

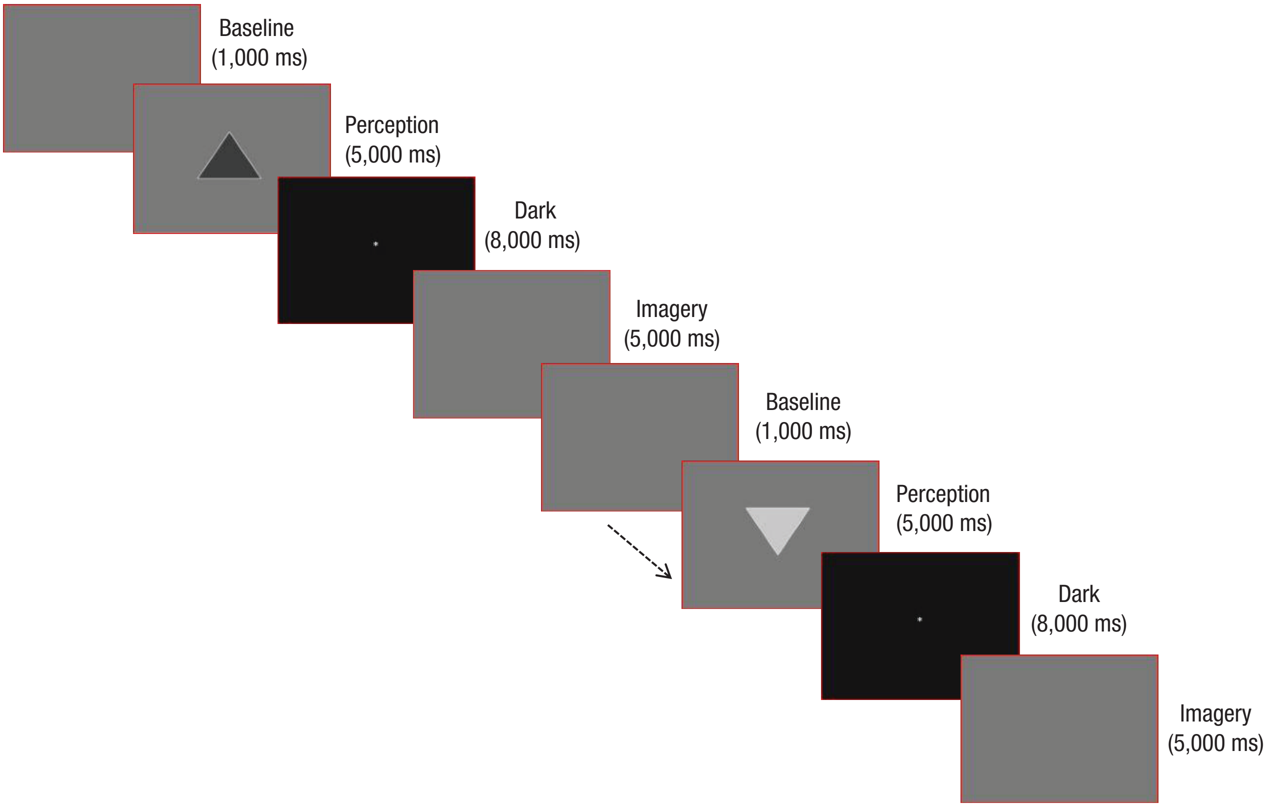

Fig. 1. Schematic illustrating the experimental paradigm. After a measurement of baseline pupil diameter during presentation of an empty gray screen, a triangle appeared. It was followed by a dark screen, and then participants imagined it while another empty gray screen was presented. Triangles could be right side up or inverted, and they varied in luminance across trials (the sequences of two successive trials are shown here).

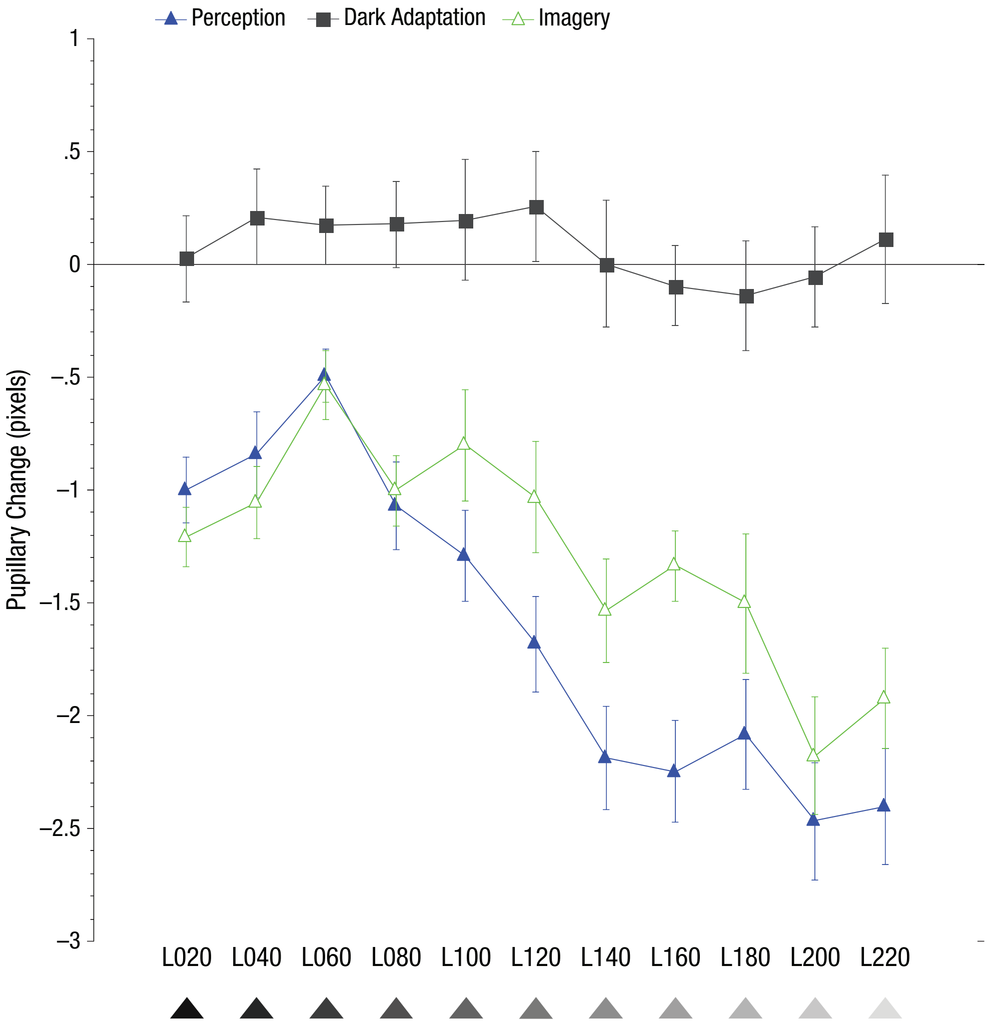

Fig. 2. Results from Experiment 1: mean pupillary-diameter change (in pixels) as a function of luminance and trial phase. Pupillary-diameter change was measured during a 5-s presentation of shapes varying in luminance (*perception phase*), during participants' 5-s imagining of the same form (*imagery phase*), and during an 8-s presentation of a dark screen (*dark-adaptation phase*). The luminance of shapes varied in 11 steps of 20 units (minimum = 20 units, L020; maximum = 220 units, L220). Error bars indicate standard errors.

analyses showed a significant correlation between pupil diameter and luminance in the perception and imagery phases, r = .83, p = .001, but not in the dark-adaptation and imagery phases, p = .11, as well as a high correlation between the physical luminance of the shape and pupillary change when imagining it, r = .80, p = .005.

Experiment 2

We presented to a new group of 18 participants (12 females, 6 males; mean age = 23.4 years; *SD* = 3.2) only triangles with the maximum and minimum degrees of lightness used in the first experiment, for a total of 24 trials. The equipment and procedure were identical to those of Experiment 1, except that there was an initial "passive" looking condition in which we recorded pupillary responses to the same stimuli and background images (luminance = 120 units in the HSL system) used during the subsequent "active" imagery condition, but without giving participants any explicit instruction to generate a mental image. However, the background's luminance was adjusted so that the mean luminance of the whole image presented on screen remained constant during the experiment (i.e., 24.3 cd/m^2).

Despite the fact that there were no changes in luminance across the images (as the pupillary responses to the passive condition clearly show; Fig. 3), during the active imagery condition, participants' pupils constricted in response to the relatively "bright" mental images but dilated in response to the relatively "dark" mental images, just as had happened during the perception phase, although to a smaller extent. A repeated measures ANOVA on the pupillary changes (in pixels) confirmed a significant interaction of condition (active, passive), image (perception, imagery), and luminance (bright, dark), $F(1, 17) = 4.58$, $p = .047$. Importantly, a paired t test confirmed the predicted difference between pupillary diameters in response to the active imagery of bright versus dark triangles, $t(17) = 5.16$, $p < .0001$. Given that the procedures of the active and passive conditions were the same except for the presence and absence of imagery instructions, these findings indicate that changes in pupil size occur as the result of an active process of imagery and not as an aftereffect or episodic trace of a previously seen picture.

Given that background luminance varied with each pattern type so that the combined luminance of the two was the same, it is interesting that the pupillary responses reflected the luminance of the pattern that was specifically requested to be imagined and not that of (either of) the backgrounds. This finding is consistent with another key feature of mental imagery, raised by Galton (1883/1907). Specifically, Galton queried, "Is the image dim or fairly clear? . . . Are all the objects pretty well defined at the same time, or is the place of sharpest definition at any one moment more contracted than it is in a real scene?" (p. 58). The common report was that attending to one or two objects would make them appear much more distinct than the others and that different objects were not clear all at once but only successively. Current accounts of imagery have concluded that whenever one generates a visual image of an object, the objects or parts of the scene are generated separately (e.g., Hebb, 1968; Kosslyn, 1980; Neisser, 1976). Thus, the present findings

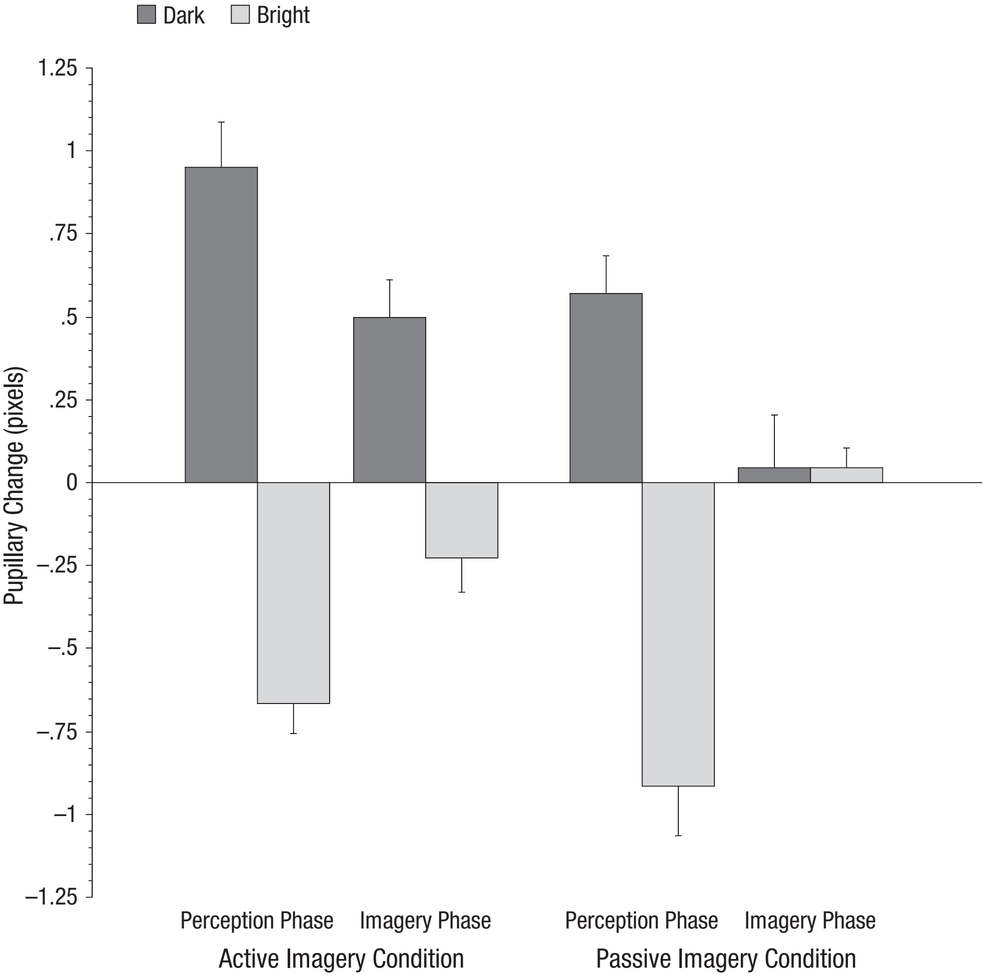

Fig. 3. Results from Experiment 2: mean pupillary-diameter change (in pixels) as a function of condition, trial phase, and luminance. Pupillary-diameter change was measured during a 5-s presentation of shapes differing in luminance (perception phase) or participants' 5-s imagining of the same forms (imagery phase). Error bars indicate +1 *SE*.

support the conclusion that it is possible to imagine a part of a scene separately from the rest of the scene while preserving perceptible qualities of the stimulus, such as its luminance. Recent image-based theories of object recognition (e.g., Poggio & Edelman, 1990) posit that object representations are closely tied to the image of an object as it was experienced, instead of consisting of illumination-invariant contour features. Thus, the present findings further support the idea that visual memory is sensitive to the illumination conditions under which an object was learned (Tarr, Kersten, & Bülthoff, 1998).

Experiment 3

The eye pupil is known to provide a reliable index of "load" on attention capacity (Kahneman & Beatty, 1966; for a recent review, see Laeng, Sirois, & Gredebäck, 2012), such that the greater the mental effort required during cognitive processing (Kahneman, 1973; Laeng, Ørbo, Holmlund, & Miozzo, 2011), the larger the pupil diameter. This fact could suggest an alternative account for an increase in pupil size corresponding to a decrease in the luminance of the imagined stimuli. Specifically, generating mental images of dark stimuli may be more effortful than generating mental images of relatively brighter stimuli. Hence, in a new experiment, we manipulated the shape complexity of the objects to be imagined and varied the brightness of the stimuli while keeping the background's luminance constant (i.e., 19.76 cd/m^2). We asked a new group of participants to generate mental images of "simple" geometrical shapes consisting of single cylinders (size = 5° of visual angle) and relatively complex geometrical shapes consisting of end-to-end assemblies of three cylinders (total size = 10° of visual angle). The cylinders' three levels of luminance, from light to dark, were 41.5 cd/m^2, 23.5 cd/m^2, and 10.1 cd/m^2. We predicted that increased shape complexity would cause participants' pupils to dilate but that the pupillary diameter in response to the imagined bright objects would be smaller than that in response to the imagined dark ones, regardless of shape complexity.

Twenty-one participants (11 females, 10 males; mean age = 23.5 years, *SD* = 3.1) saw each shape presented twice for 5 s, in a fixed pseudorandom order, at three levels of brightness (dark, medium, and bright), for a total of 12 trials. Immediately after each imagery trial, participants were asked to report how effortful it was to visualize each specific shape; responses were made using 5-point scales (−2 = *very low effort*, −1 = *low effort*, 0 = *neither low nor high effort*, 1 = *high effort*, 2 = *very high effort*). These data were used as a subjective measure of mental effort in relation to objective differences in the shapes' complexity and luminance.

A repeated measures ANOVA with shape (simple, complex), luminance (dark, medium, and bright), and condition (perception, imagery) as within-subjects factors and pupillary change (in pixels) as the dependent variable revealed significant interactions between condition and luminance, $F(2, 38) = 3.37$, $p = .045$, as well as between condition and shape, $F(2, 38) = 6.34$, $p = .021$. The effects of luminance and complexity were additive, as reflected by the fact that the three-way interaction of condition, shape, and luminance failed to reach significance, $F(2, 38) = 0.58$, $p = .61$. Figure 4 illustrates, in the top panel, changes in pupil diameter during the perception and imagery phases for different levels of object brightness and, in the bottom panel, changes in pupil diameter during the perception and imagery phases for the two levels of shape complexity. Importantly, paired *t* tests confirmed that participants' pupils constricted in response to bright shapes (mean change = −0.34; *SD* = 0.80) compared with dark shapes (mean change = 0.32; *SD* = 0.80), $t(19) = 3.37$, $p = .003$, and medium-bright shapes (mean change = −0.09; *SD* = 0.90), $t(19) = 1.98$, $p = .05$. With regard to shape complexity during perception and imagery, results showed an increase in pupil size from the perception phase (mean change = −0.58; *SD* = 0.65) to the imagery phase (mean change = 0.27; *SD* = 0.91) for complex shapes, $t(19) = 3.41$, $p = .003$, but not for simple shapes (perception phase: mean change = −0.24; *SD* = 0.65; imagery: mean change = −0.22; *SD* = 0.87), which is indicative of increased mental effort when imaging the more challenging shapes.

Mean ratings of mental effort during imagery were analyzed using repeated measures ANOVA with shape (simple, complex) and luminance (dark, medium, and bright) as within-subjects factors. This revealed only a main effect of shape complexity, $F(1, 19) = 19.90$, $p = .0003$. Specifically, simple shapes yielded lower ratings for effort (dark: $M = -0.86$; medium: $M = -0.88$; bright: $M = -.64$) than did complex shapes (dark: $M = 0.18$; medium: $M = -0.05$; bright: $M = -0.05$). Clearly, there was no indication in these subjective measures that the shapes' levels of luminance required differing levels of mental effort during imagery.

Experiment 4

A critique often levelled at imagery studies is that participants may comply with task demands or experimenters' expectations and adjust their responses according to the hypotheses (e.g., Intons-Peterson, 1983). Thus, our participants may have guessed the aim of each experiment and, if equipped with knowledge on how to indirectly influence pupillary responses, they may have modified their pupil diameters accordingly. Engaging in

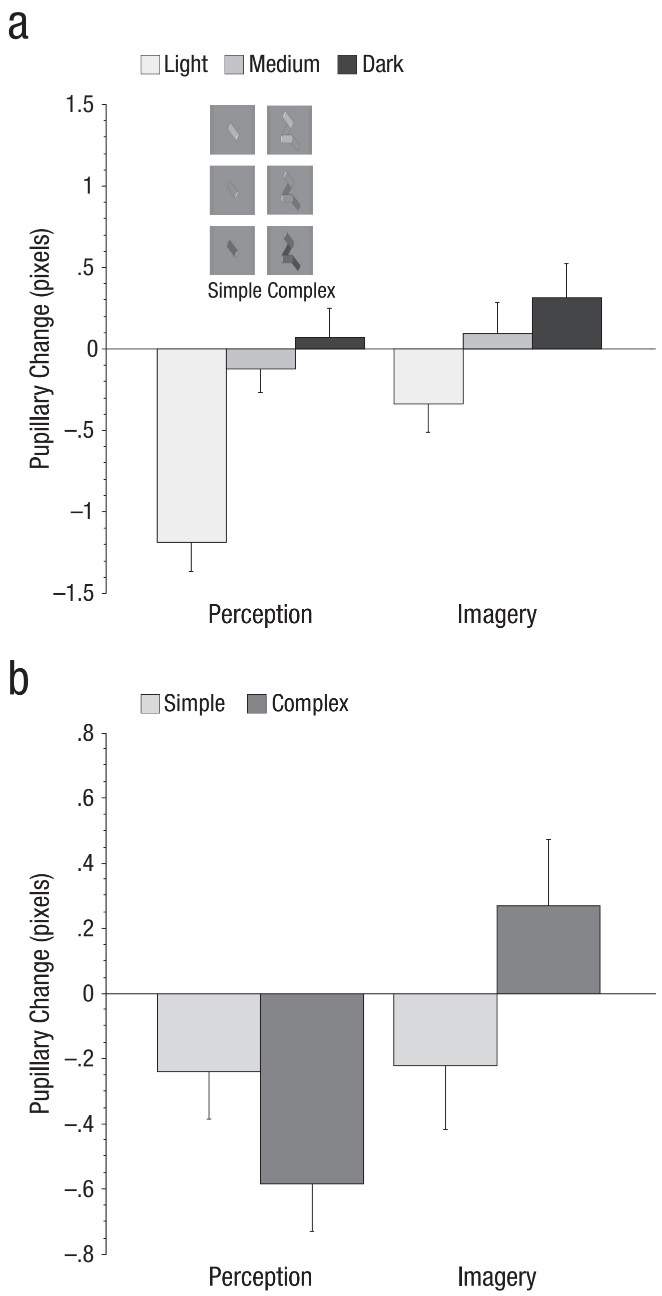

Fig. 4. Results from Experiment 3: mean pupillary-diameter change (in pixels) as a function of trial phase and luminance (top panel) and as a function of trial phase and complexity (bottom panel). Pupillary-diameter change was measured during a 5-s presentation of shapes differing in luminance or participants' 5-s visualization of the same forms (imagery phase). The inset shows each of the six shapes (combinations of the three levels of luminance and two levels of complexity) used as stimuli. Error bars indicate +1 *SE*.

mathematical computations (Hess, 1972) or thinking about emotionally intense situations can lead to pupillary dilations (e.g., Whipple, Ogden, & Komisaruk, 1992). Using this knowledge, one could indirectly cause the eye pupil to "dilate" by engaging in complex problem solving or conjuring up emotionally laden mental content (Ekman, Poikola, Mäkäräinen, Takala, & Hämäläinen, 2008), although it does not seem possible that one could use such strategies to also "constrict" the pupil below the level already elicited by the current ambient light (Loewenfeld, 1993). However, voluntarily changing one's eyes' vergence and accommodation can cause the pupil diameter to decrease (Hess, 1972). Moreover, visual feedback based on changes in the appearance of the display could, in principle, be used when attempting to explicitly control the pupil diameter (i.e., the same object may appear brighter when the pupil size is larger and darker when it is smaller).

Although it seems unlikely that our participants would have specific knowledge about these strategies and be able to use them effectively while guessing the experiment's specific predictions, we decided to test the participants from the previous experiment in an additional task, in which they were explicitly requested to either "enlarge" or "reduce" the size of their pupils following a command. There were a total of 16 trials, and for half of these, the participants attempted to control their pupils while looking at an empty gray screen (19.76 cd/m^2) for 7 s. On the other half of the trials, the participants could see the white outline of a triangle (size = 4° of visual angle) in the center of the same gray background. Trials were ordered according to a pseudorandom sequence.

Pupillary diameters were analyzed in an ANOVA with condition (baseline, dilate to blank, dilate to shape, constrict to blank, constrict to shape) as a within-subjects factor. There was no significant difference among the various conditions, $F(4, 84) = 1.02$, $p = .40$, and no indication that forcing the pupil to dilate (dilate to blank: M = 5.0 mm; SD = 0.7; dilate to shape: M = 5.0 mm; SD = 0.7) resulted in larger diameter than when attempting to constrict it (constrict to blank: M = 5.0 mm; SD = 0.7; constrict to shape: M = 5.0 mm; SD = 0.7) or that this could be accomplished on the basis of visual feedback from a shape present in the display. Thus, the same participants who had previously shown clear-cut pupillary adjustments to imagined objects of different levels of brightness were completely unable to comply with the explicit experimental demands and adjust their pupils at will. This finding confirms the prevailing idea that human beings cannot directly control the size of their eye pupils (Loewenfeld, 1993) and that pupillary changes either above or below the level of "reflexive" adjustments to physical light may occur only indirectly (e.g., by mentally recreating a situation that, in the real world, would elicit a change in the size of the pupil).

Experiment 5

In a final experiment, we tested the possibility that pupillary adjustments can occur when any sort of mental images are conjured up and not only during the imagining of a scene just experienced and held in short-term memory. Hence, we recruited a new group of 52 participants (25 females, 27 males; mean age = 24.6 years, *SD* = 4.1) and asked them to imagine some familiar situations while looking, in all cases, at the same empty gray screen used previously. Each trial was initiated by the participant with a key press, which caused the baseline empty screen to appear for 1,000 ms. Following this, the scenarios to be imagined were described in simple words presented in the center of the screen. The participant pressed the space bar when he or she had the requested image in mind, which initiated a 7-s recording of pupil size while the participant looked at the empty screen, followed by another slide displaying the word "stop." Participants were asked to imagine that they were "looking at the night sky," "looking at a sunny sky," "looking at a cloudy sky," or "in a completely dark room." To elicit imagery of a specific object, we asked each participant to also imagine seeing the "face of their mother," either as seen in full sunlight or as seen in shadow.

In addition, the last 21 individuals (11 females, 10 males) who participated in the experiment were queried after each imagery trial to report how effortful it was to generate each specific scenario in their mind, using the same 5-point scale described earlier. These data were collected to assess whether reminiscing about dark scenarios could require more effort than reminiscing about bright ones. At the end of the experiment, the participants were asked to write in their own words what they believed was the goal of the study.

There were clear and significant changes in pupillary diameter related to changes of light ambience in the bright and dark directions (Fig. 5)—that is, respectively, constrictions (pupillary changes below baseline) and dilations (pupillary changes above baseline). A repeated measures ANOVA on pupillary changes with imagined scenarios as the within-subjects factor confirmed that the items caused different shifts in pupil diameter, $F(5, 255) = 9.93$, $p < .0001$. Post hoc Fisher's protected-least-significant-difference tests showed that while participants reminisced about a sunny sky, their pupils were smaller than when they reminisced about a night sky, $p = .001$, or a cloudy sky, $p = .0001$, and smaller than when they imagined a dark room ($p = .0001$) or their mother's face in shade ($p < .0001$). However, imagining a dark room was associated with larger pupils than was imagining a night sky, $p = .009$. Moreover, pupils constricted in response to imagining a face in sunlight compared with a face in shade, $p = .01$, or a dark room, $p = .0001$, as well as a cloudy sky, $p = .001$.

Interestingly, in Galton's (1883/1907) original collection of informants' reports, one of the participants wrote: "I feel as though I was dazzled, e.g., when recalling the sun to my mental vision" (p. 61). The present results clearly provide, for the first time, a strong and objective foundation to this type of mental experience. More recently, Naber and Nakayama (2013) and Binda, Pereverzeva, and Murray (2103) measured the pupil responses of observers viewing photos of landscapes and found that the observers' pupils constricted more in response to images containing a sun than to those containing a moon, and this effect was stronger when the pictures were seen upright instead of upside down. Taken together, these findings strongly suggest that the pupil adjusts to a high-level interpretation of image content, regardless of whether a "bright" image is perceived or just imagined.

To assess whether items of different brightness could be associated with different degrees of mental effort, we averaged the effort estimates for dark (night sky, cloudy sky, face in the shade, dark room) and bright (sunny sky, face in the sun) items. On average, participants' estimates of mental effort were in the low range, and there was no indication that dark scenarios ($M = −0.23$, $SD = 0.82$) were more difficult to imagine than bright ones ($M = −0.19$, $SD = 0.98$), which was also confirmed by a repeated measures ANOVA, $F(1, 20) = 0.044$, $p = .84$. Finally, a simple regression analysis, with reported effort for each trial as the predictor and pupillary change as the predicted variable, revealed a positively sloped relationship ($y = 0.14 + 0.06x$), which, however, failed to reach significance, $t(125) = 0.59$, $p = .55$. Hence, we conclude that mental effort could not possibly account for the observed changes in pupillary adjustments to the various scenarios.

Finally, only 2 participants out of 21 wrote in response to the query about the goal of the study that it likely investigated changes in the size of the pupil during imagery, and neither of these 2 individuals mentioned specific predictions (e.g., in relation to luminance). The majority of participants either believed it to be a study on the role of eye movements in memory or simply had no idea. The low proportion of participants who mentioned pupillary responses during imagery renders implausible the argument that the group's performance reflected compliance with expectations about the study.

Discussion

We predicted that a simple act of imagining forms or scenes would evoke adjustments of the eye pupils

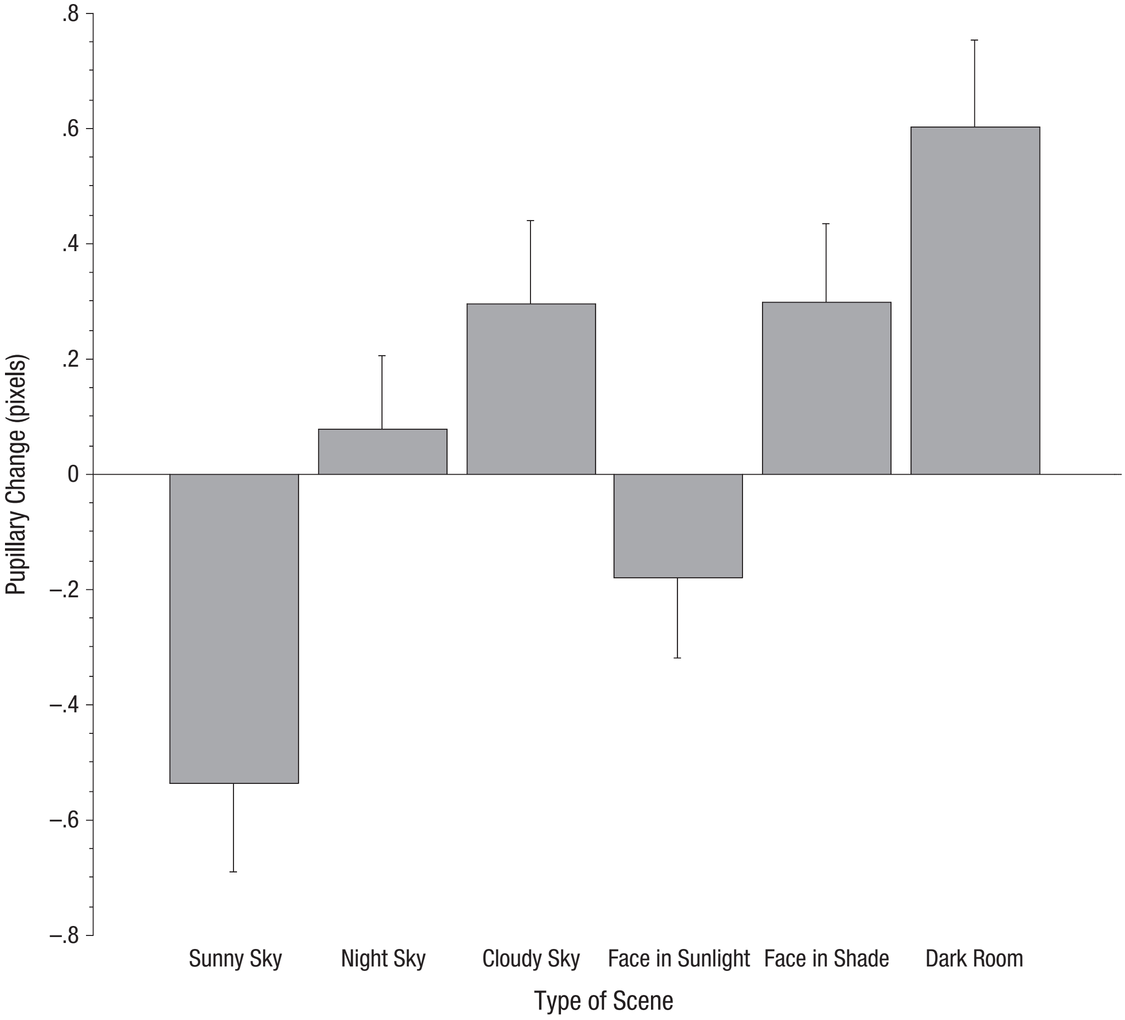

Fig. 5. Results from Experiment 5: mean pupillary-diameter change (in pixels) during participants' 7-s imagining of a scene, as a function of the type of scene. Error bars indicate +1 *SE*.

comparable to those elicited during their perception. This expectation was based on the assumption that the eye pupil can be controlled by an individual's subjective perceptions of brightness, instead of merely automatically responding to the physical energy of light. In fact, the eye pupil also constricts in response to illusions of brightness (Laeng & Endestad, 2012), which indicates that inputs from higher brain functions, such as those responsible for interpreting what one sees, which have been shaped by repeated encounters with image sequences (Purves, Wojtach, & Lotto, 2011), do play a role in fine adjustments of the eye pupil. Generally, the perception of light is not straightforwardly related to physical parameters, as indicated by the simultaneous-brightness-contrast phenomenon (Purves & Lotto, 2011). In fact, pupillary adjustments that reflect concurrent visual strategies could be more adaptive than those based on physical stimulus features, and we surmise that the pupillary constriction in response to illusions of brightness is designed to protect the eye's sensitive light-absorbing cells from potentially damaging levels of light that the brain, given the available information, judges to be probable. Similarly, we believe that a pupillary response to imagined light could reflect the adaptive role played by mental imagery, which is capable not only of "reconstructing" the past but also of anticipating what may occur in the near or distant future (Moulton & Kosslyn, 2009).

In recent years, neuroimaging studies have supported the idea that imagery is a conscious "rerepresentation" of a previous perceptual brain state, because the pattern of activity within the visual cortex during the perception of an object and the later imagining of it is nearly identical (Ganis, Thompson, & Kosslyn, 2004) and specific to the domain of the object (O'Craven & Kanwisher, 2000). In addition, consistent with the idea that mental images preserve perceptible qualities, results of eye-tracking studies have shown that engaging in visual imagery can trigger a sequence of oculomotor adjustments over the positions of imagined objects, similar to those used in perceptual scrutiny of the objects, despite their absence in the external world (e.g., Laeng & Teodorescu, 2002). Findings from studies using the binocular-rivalry paradigm also suggest that visual imagery involves low-level mechanisms that overlap with visual perception (Pearson et al., 2008) and that luminance is among these candidate low-level features, given that generating or maintaining a mental image over a background of different luminance reduces the image's priming effect during a subsequent perceptual-rivalry task (Sherwood & Pearson, 2010).

Because we have shown that the eye pupil automatically adjusts to the strength of imagined light and does not simply reflect the current ambient light, we conclude that a mental image rerepresents sensory information gathered from previous experience, including the luminance of the visualized scenario. In previous studies, researchers who have measured pupillary size during imagery have not specifically compared this variable to either measured or hypothesized levels of physical luminance of the imagined scenes but have simply measured pupillary change during the act of generating mental images against a neutral baseline (e.g., Reeves & Segal, 1973). Moreover, the present results cannot be accounted for by changes in the pupil caused by mental effort, given that both objective and subjective levels of effort did not vary for shapes of different luminance. Finally, we can rule out the possibility that our participants controlled their pupil sizes, either directly or via some cognitive strategy, to comply with experimental expectations. In fact, they were not able to directly control pupil diameters when explicitly requested to do so and, in general, they appeared completely naive about the specific hypotheses of the study. Thus, we conclude that the existence of physiological (pupillary) changes in response to imaginary light supports a strong rejection of "nihilistic" criticisms of imagery (cf. Kosslyn, Ganis, & Thompson, 2003), according to which similar responses to images and perceptions are accounted for by participants' simulating expected behavior without necessarily rerepresenting a perceptual experience.

Author Contributions

B. Laeng and U. Sulutvedt developed the study concept. Both authors contributed to the study design. Testing and data collection were performed by U. Sulutvedt. B. Laeng performed the data analyses. Both authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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