

Bright illusions reduce the eye's pupil

Bruno Laeng¹ and Tor Endestad

Department of Psychology, University of Oslo, 0317 Oslo, Norway

Edited by Dale Purves, Duke University Medical Center, Durham, NC, and approved December 22, 2011 (received for review November 9, 2011)

We recorded by use of an infrared eye-tracker the pupil diameters of participants while they observed visual illusions of lightness or brightness. Four original illusions [based on Gaetano Kanisza's [Kanizsa G (1976) *Subjective contours*. *Sci Am* 234:48–52] and Akiyoshi Kitaoka's [Kitaoka A. (2005) *Trick Eyes* (Barnes & Noble, New Providence, NJ).] examples] were manipulated to obtain control conditions in which the perceived illusory luminance was either eliminated or reduced. All stimuli were equiluminant so that constrictions in pupillary size could not be ascribed to changes in light energy. **We found that the pupillary diameter rapidly varied according to perceived brightness and lightness strength.** Differences in local contrast information could be ruled out as an explanation because, in a second experiment, the observers maintained eye fixation in the center of the display; thus, differential stimulation of the fovea by local contrast changes could not be responsible for the pupillary differences. Hence, the most parsimonious explanation for the present findings is that **pupillary responses to ambient light reflect the perceived brightness or lightness of the scene and not simply the amount of physical light energy entering the eye. Thus, the pupillary physiological response reflects the subjective perception of light and supports the idea that the brain's visual circuitry is shaped by visual experience with images and their possible sources.**

Adjustments of the size of the eye's pupil occur automatically in response to changes in the intensity or energy of light (1). One type of response, named the pupillary light reflex, is mediated by the parasympathetic system and protects the retinal receptors by constricting the pupil and reducing excessive light energy. Sympathetically mediated pupillary dilations seem equally functional, because they increase the field of view and the light available from potentially critical object surfaces and are therefore beneficial to attentive, exploratory (2), and visual processing as well as enhancing preparation for "fight or flight." These pupillary responses are omnipresent in animals possessing optical lens eyes and are controlled by a dedicated neural subcortical network that can rapidly react to changes in light. Such a network appears to operate like a closed-loop servomechanism (3) and is often described as independent from the (mainly cortical) parts of the visual system that interpret light energy information.

The view that fast pupillary adjustments to light reflect the operation of a separate subcortical neural network would seem supported by the clinical observation that in patients whose visual cortex is completely damaged and who have lost all conscious visual perception, the pupils continue to respond to sudden changes in room illumination (4). Based on such a classic view, one could be led to expect that reflexive adjustments of the pupil to light should be impervious to our subjective sense of luminance. In fact, one would expect that light intensity and pupillary diameters would be proportional and highly correlated. In simple words, the eye's pupil should not be prepared to respond to any other visual property than the sheer amount of physical light energy entering the eye at a particular moment. However, we present here evidence that the motor response of pupillary constriction can reflect the subjective sense of the amount of light originating from a specific image. To reveal this, we took advantage of visual illusions, where the physical luminance of the stimulus and our perception of its luminance do not match.

Specifically, our observers viewed equiluminant images where the actual physical energy entering the eye remained constant, and yet for some of these images (Fig. 1) observers invariably reported a strong impression of either lightness (i.e., a lighter

appearance of an object surface, which in the present case of the Gaetano Kanisza figures is also illusory) (5, 6) or brightness (the brighter appearance of a source of light, which in the present case of the Akiyoshi Kitaoka figures is also illusory (7); <http://www.ritsumei.ac.jp/~akitaoka/index-e.html>). In fact, despite one region of the stimulus (e.g., the hole in the center of the Asahi shape in Fig. 1) appearing brighter than the background, both images have the same luminance in physical terms. Similarly, although the brighter, ghostly white triangles in the Kanisza illusions may be clearly evident to human observers, they are completely invisible to a photometer or image scanner (8).

Our hypothesis is that the pupillary motor response is susceptible to illusions of lightness and brightness. This idea is based on several considerations. First, within contemporary accounts of visual perception (9, 10), the brain's visual circuitry is shaped by successfully guided behavior and, consequently, the world is represented in a fundamentally probabilistic manner on the basis of accumulated experience with images and their possible sources. Indeed, our perception of lightness or brightness does not straightforwardly relate to physical parameters, as indicated by the simultaneous brightness contrast phenomenon; if so, it would be more adaptive if pupillary adjustments reflected concurrent visual strategies instead of physical stimulus features.

Second, the classic account of pupillary light reflex as a closed loop and impenetrable servomechanism has been recognized as a simplification (3). In fact, several studies show that subtle pupillary constrictions can also be measured after changes in shape information or color content of stimuli that do not change in luminance (11–13). These subtle pupillary responses to equiluminant stimuli may require the processing of specific stimulus attributes within higher visual networks (e.g., extrastriate visual cortex), which would then provide feedback and modulate the pupillary adjustments.

Finally, we expect that such a pupillary response to illusory lightness or brightness can occur fast (or faster than typical cognitive influences on the pupil diameter) (14, 15). The transfer time in the macaque brain from the brainstem nuclei that control pupillary responses to the occipital cortex and from there to the frontal lobes and back to the brainstem nuclei could occur in ~150–200 ms (16). Studies of event-related potentials (ERPs) in humans have indicated that, for complex visual decisions on shapes (e.g., when an observer decides whether she is looking at an animal or not), ERPs to target and distractor images diverge strongly at ~150 ms (17). Moreover, single-unit recordings in the anterior temporal cortex of macaques have shown selectivity to exemplars of the target category (tree) as early as 80–90 ms after stimulus presentation (18). Neurons in the inferotemporal cortex of monkeys also respond selectively to faces of humans or monkeys after only 100 ms (19, 20). Also, several cognitive processes (e.g., speech comprehension), which are clearly dependent from cortical areas, have been estimated to influence oculomotor reactions (e.g., a saccade) within a time window of only 100 ms (21). Remarkably, animal studies suggest that neurons in area V1 of the visual cortex show very early responses that are correlated with brightness, the Cornsweet illusion, and lightness constancy

Author contributions: B.L. and T.E. designed research; B.L. and T.E. performed research; B.L. and T.E. analyzed data; and B.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: bruno.laeng@psykologi.uio.no.

(22, 23). If such an early visual area like V1 performs critical brightness computations in animals, it might play a similar role in humans (24). In sum, we surmise that adaptive feedback mechanisms that are likely to occur early in the occipital cortex could underlie rapid pupillary constrictions to objects that appear to shine, glare, luster, or glow. Moreover, pupillary constrictions against probable strong illumination sources would constitute a clear biological adaptation of the visual system (as a protective response).

To test the above hypothesis that the pupillary motor response is susceptible to illusions of lightness and brightness, we selected four visual illusions that originate from available examples created by Kanisza or by Kitaoka. The Kanisza illusions represent classic examples of illusory contours, where observers typically see an illusory shape (i.e., a triangle or square in our examples) that appears to overlap the other, high-contrast inducing shapes. In addition to seeing an “extra” shape, observers typically attribute to it a whiter-than-white uniform lightness. A simple planar rotation of the inducing shapes (e.g., the “Pacmen” of the Kanisza triangle) completely eliminates both the perception of the illusory contours forming the shape and of the difference in light intensity with the background. The other two Kitaoka illusions yield a remarkable effect of illusory brightness but they also differ from the Kanisza illusions in several interesting respects. First, these images appear to glow or glare on sides of the depicted objects (i.e., in the light of cubes illusion) and a bright light or a backlit effect outside the figure is visible (e.g., from a hole within the shape in the Asahi, or morning sunlight figure). Given that the subjective strength of the illusory brightness seems greater in figures that glare (as the Kitaoka figures) than in matte-like surfaces (as the Kanisza figures), a prediction of this study is that the present Kitaoka figures will be more likely than the Kanisza

figures to yield pupillary adjustments (i.e., constriction) to the illusory changes in brightness.

Therefore, we recorded by use of an infrared eye-tracker the pupil diameters of participants while they observed the above-described visual illusions of brightness. In addition, we manipulated the original illusions so as to obtain control conditions in which the perceived illusory brightness was either eliminated or reduced. All stimuli were equiluminant so that constrictions in pupillary size could not be ascribed to changes in light energy.

Results

Experiment 1. Separate repeated-measures analyses were performed for each of the four illusion types. The analysis on the Asahi illusion revealed a main effect of picture, $F(3, 42) = 7.4$, $P < 0.005$. The original picture (A) caused a clear pupil constriction (mean change = -0.202 mm; SD = 0.16) compared with baseline. Post hoc Student–Newman–Keuls tests showed that pictures A and B differed significantly (mean difference = 0.18; critical difference = 0.15), as did picture A vs. D (mean difference = 0.16; critical difference = 0.14). Fig. 2 *Upper Left* illustrates the average pupillary change for each picture. Fig. 3 *Upper* shows the pupillary change over the recording period for the picture that was judged to be brightest (A) vs. the one judged to be least bright (B). It can be seen from Fig. 3 that within the first 100–200 ms from onset of the picture (time 0), the pupil constricts and then it gradually dilates over time, although remaining smaller than baseline ~ 2 s or longer. More interestingly, the pupil diameter remains at all times smaller for the original illusion (A) than for the version manipulated to appear as less bright (B).

The analysis on the light of cubes illusion approached significance, $F(3, 42) = 2.3$, $P < 0.08$. The original image (A) showed the greatest pupil constriction (mean change = -0.24 mm;

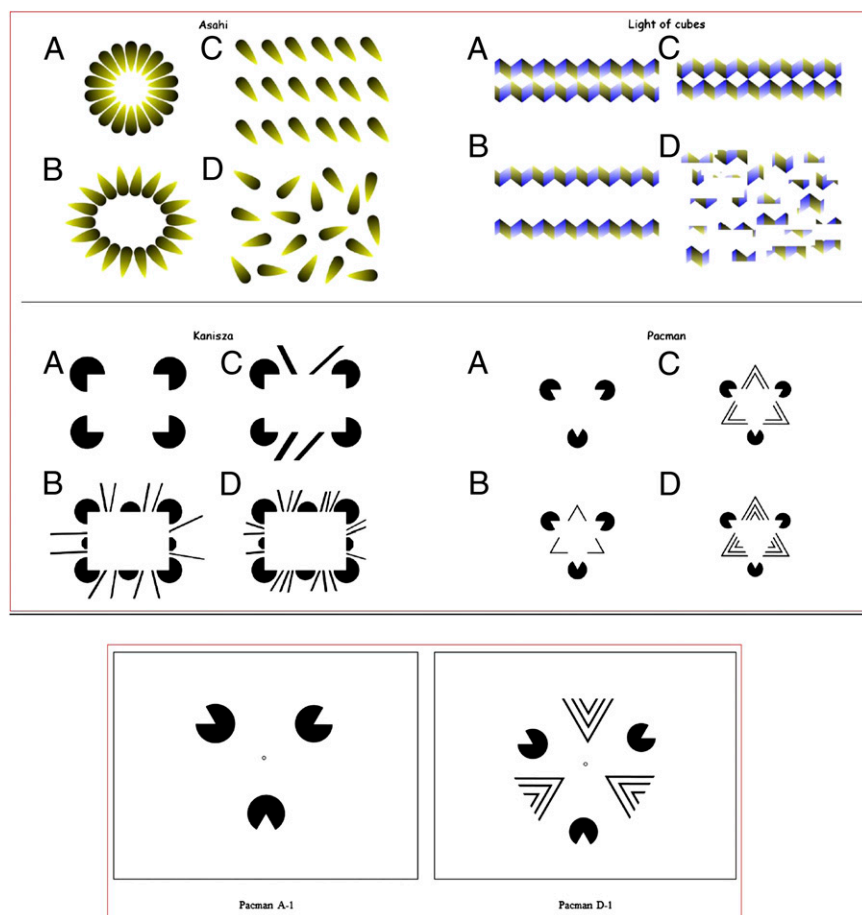


Fig. 1. (*Upper*) The four figures (Asahi, light of cubes, Kanisza, Pacman) in the four versions used in the experiments (A–D). For the Asahi and light of cubes, version A images are the originals, and they are typically reported as generating a strong impression of brightness or glare on the central regions of the figures. For the Kanisza and Pacman figures, there is a progressively (from A to D) increased impression of lightness of the illusory central shape. (*Lower*) Additional control figures used in experiment 2 for Pacman A and D, where the Pacman shapes are rotated so as to destroy the illusion of a central triangular form of lighter color.

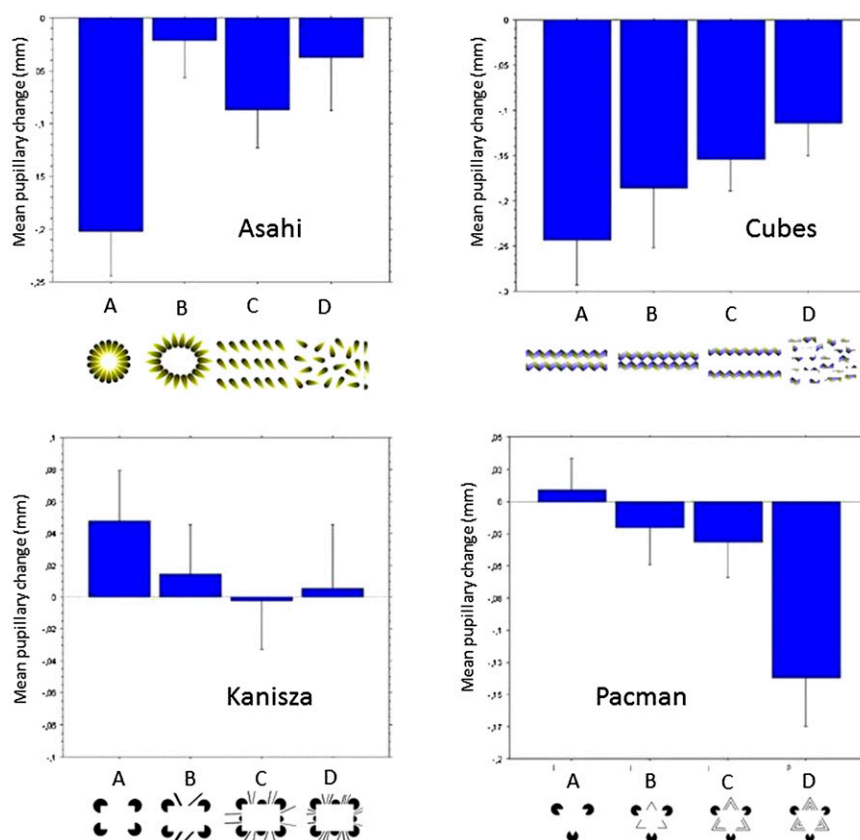


Fig. 2. Changes in mean pupil diameters (in mm) for each of the four types of illusions, averaged over a 4-s epoch from onset. Bars indicate SEs.

SD = 0.19). Fig. 2 *Upper Right* illustrates the mean pupillary change for each version over the whole recording period. Because we had predicted that the subjectively brighter pictures should cause greater constrictions than less bright pictures, we directly tested with a paired t test the pupillary responses to the original picture (A) that was ranked as brightest by our independent judges against picture D. This comparison revealed that constrictions to picture A were, in fact, greater than those to picture D, $t(14) = 2.9$, $P = 0.011$.

The analysis on the Kanisza illusion failed to reveal a main effect of picture, $F(3, 42) = 0.8$, $P = 0.51$. On average, the pupils appear to slightly dilate from baseline (Fig. 2, *Lower Left*, and Fig. 3). In contrast, the analysis on the Pacman illusion revealed a main effect of picture, $F(3, 42) = 6.2$, $P = 0.001$. We expected that the illusory triangular shape should appear as progressively lighter from picture A to picture D and indeed, we observed progressively smaller pupil diameters (Fig. 2, *Lower Right*). According to post hoc Student–Newman–Keuls tests, pupils were smaller for picture D (mean change = 0.005 mm; SD = 0.180) than for A (mean difference = 0.15; critical difference = 0.11), as well as pictures B (mean difference = 0.12; critical difference = 0.10) and C (mean difference = 0.11; critical difference = 0.09). Fig. 3 *Lower* shows the pupillary change time course over the recording period.

Finally, we analyzed eye movement data by obtaining an average count of the number of saccades that occurred over all versions of the illusions. These data were collapsed and analyzed by ANOVA with illusions (Asahi, Cubes, Kanisza, Pacman) as the independent variable. The analysis showed a significant effect, $F(3, 51) = 32.5$, $P < 0.0001$, and paired t tests revealed that the cubes figures [$5.3 < t(16) < 10.1$] provoked the largest number of saccades (mean = 12.4; SD = 0.9) compared with all other figures (Asahi: mean = 10.2; SD = 0.8; Kanisza: mean = 10.9; SD = 1.1; Pacman: mean = 9.9; SD = 0.4).

Experiment 2. It is known that the fovea and its immediately surrounding area can contribute more than the rest of the retinal field to the pupillary response to luminance (25, 26). Thus, in a second experiment, we asked a new group of participants to maintain fixations at the center of the screen. Only those two versions of each illusion that in the previous experiment had produced maximum and minimum pupillary changes were included. To demonstrate that the present effects occur rapidly, and to make sure that these effects are not dependent from the presence of eye movements, we recorded pupillary changes only within the first 300 ms from each illusion's onset. We also created two control conditions for one of the Kanisza illusions in which the Pacmen inducing the illusory surface were rotated, so as to eliminate the perception of the surface and with it of its increased lightness while maintaining unchanged the physical luminance of the images. Finally, we measured the psychometric function for each participant's perceived lightness/brightness in a separate session, where these same participants were asked to indicate which of two adjacent pictures was perceived as stronger in luminance for all variants within each class of illusion. This procedure establishes a relative probabilistic function for each comparison. Fig. 4 shows the mean ratings for each illusion based on this function side by side to the changes in pupillary diameters.

The analysis on the Asahi illusion revealed a main effect of picture, $F(1, 30) = 7.5$, $P < 0.01$. The original illusion (A) caused a larger pupillary constriction (mean change = -0.412 mm; SD = 0.26) compared with picture D (mean change = -0.322 mm; SD = 0.21). The analyses on ratings confirmed that Asahi A was rated as significantly brighter than D, $F(1, 30) = 18.7$, $P < 0.0002$ (Fig. 4, *Upper Left*). Similarly, for the light of cubes illusion, there were significantly larger constrictions, $F(1, 30) = 18.1$, $P < 0.0002$ (Fig. 4, *Upper Right*), for the original illusion A (mean change = -0.49 mm; SD = 0.24) than for version C (mean change = -0.304 mm; SD = 0.26). As found also in the previous experiment, the

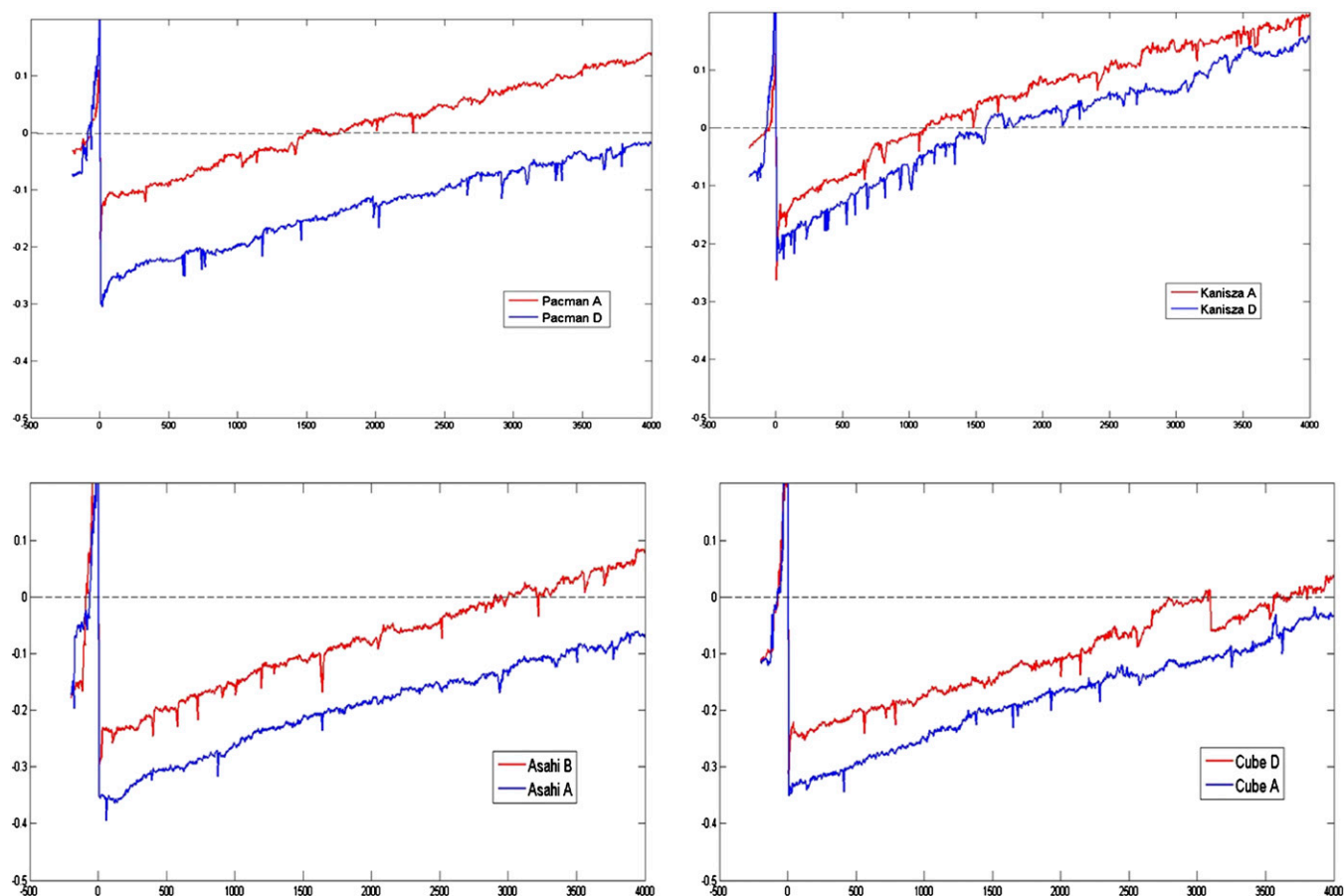


Fig. 3. Mean pupillary diameter in millimeters over time in milliseconds (time 0 = image onset) for the two images causing the smallest and the largest pupillary changes. Note that, in all cases, the smallest pupillary diameters occurred when viewing the original illusions.

analysis on the Kanisza illusion failed to reveal a main effect of picture, $F(1, 30) = 0.9$, $P = 0.35$ (Fig. 4, *Lower Left*). Interestingly, the psychophysics supports the idea that the two images differ only marginally in their perceived lightness, $F(1, 30) = 4.6$, $P = 0.04$. The analysis on the Pacman illusions revealed a marginally significant main effect of picture, $F(3, 90) = 2.71$, $P = 0.05$. More importantly, when the two Pacman illusions A and D were compared with their respective control conditions, A-1 and D-1 (Fig. 1, *Lower*), as well as to each other, Pacman D, which had received the highest lightness ratings, differed significantly ($P < 0.01$) from both its control figure and Pacman A. A repeated-measures ANOVA on the psychophysics revealed a significant difference in the perceived lightness of the images, $F(3, 90) = 3.7$, $P = 0.01$; as shown in Fig. 4, Pacman D was rated the lightest and Pacman A the image with the least lightness.

Discussion

The present findings show that illusions of brightness or lightness can cause pupillary constrictions from an equiluminant baseline. Importantly, the various versions of the illusions resulted in pupillary constrictions in amounts proportional to their perceived luminance, despite that the physical luminance remained unchanged from one version to another. However, the Kanisza illusion yielded no significant changes in pupillary diameter in two separate experiments, which was consistent with its low degree of subjective lightness.

That these illusions can result in pupillary constrictions is remarkable, given that eye-catching stimuli typically produce a dilation of the eye pupil. In fact, a great deal of research has revealed that pupil size visibly increases when viewing attention-grabbing

stimuli, despite constant illumination and no changes in ocular accommodation (27, 28). These studies have led to the proposal that an event-related increase of pupil size or dilation represents a physiological marker of use of attentional resources (28–31). For example, Einhäuser et al. (16) have shown that pupillary dilations were phase locked to switches between conscious percepts of bistable figures (e.g., the Necker cube). Thus, we would expect that the presentation of our stimuli concomitantly caused a pupillary dilation. If so, dilations would counteract to some extent the pupillary constrictions due to the subjective perception of lightness/brightness. The Asahi figure, being subjectively very bright, might constitute a stimulus that is particularly powerful in provoking a pupillary constriction over and above the presence of counteracting pupillary dilations due to attentional processes.

Because our stimuli were all equiluminant, any changes in pupillary diameter could not be attributed to changes in mean luminance of each whole image. The Kitaoka figures were obtained by simply translating on screen the shape elements, so that the Michelson contrast of these images clearly remained constant. It could be argued, however, that local band-limited contrast did change in these images, and this would result in different incremental and decremental luminance changes from the local background. If one takes into consideration also that the fovea and its surrounding area, approximately extending up to 10° of visual angle (26), contributes more than the rest of the retinal field to the pupillary response to luminance (25), then depending on which region of the image the observers fixate, different levels of local contrast would stimulate the central regions of the retina. Indeed, pupillometric studies in humans and monkeys have shown that small pupillary constrictions can be reliably measured also to changes in local contrast, color content, and spatial frequency of

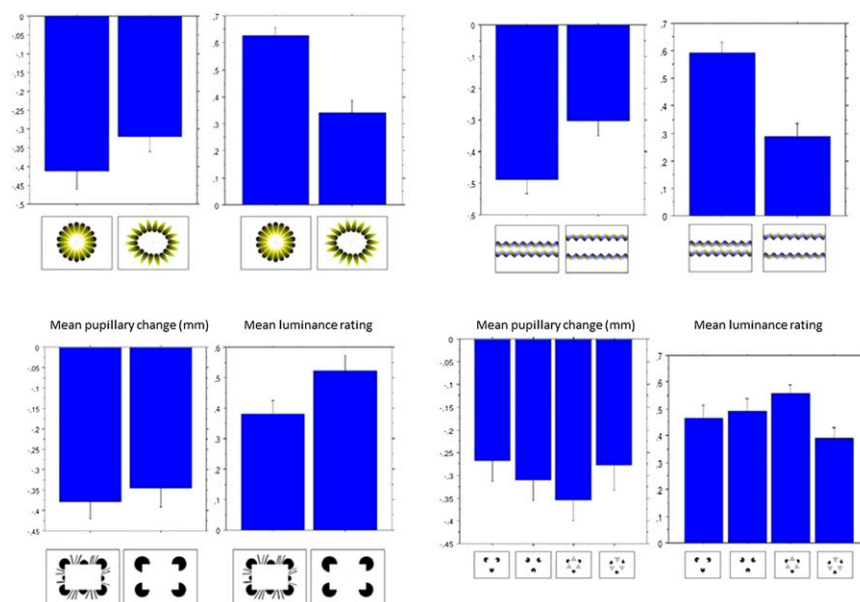


Fig. 4. The first pair of columns in each set represents the mean changes in pupil diameters (in millimeters) for each of the four types of illusions, averaged over a 200-ms epoch from onset. The second pair of columns in each set represent mean ratings of luminance (lightness/brightness) matching within each type of illusion, expressed as a relative probabilistic function for each picture comparison (e.g., 0, darker; 1, lighter, where 0.50 indicate no relative difference). All bars indicate SE.

images that keep the same overall brightness. This phenomenon has been exploited, for example, in research with blindsight patients, by showing small pupillary constrictions to the slow appearance of equiluminant gratings within the patient's blind field (32). As Fig. 5 illustrates, our observers spent about half of the fixation time at the center of the image (where the subjectively stronger light is located or, for the lightness illusion, over an invisible edge), but during the rest of the time they did fixate the figures' elements, which are always darker than the background. Thus, in the second experiment, we controlled eye position by enforcing fixation and examining pupillary data in a time window of 300 ms from pictures' onset so as to rule out possible confounds due to the factors detailed above. Interestingly, these enforced-fixation data strongly confirmed the presence of the previously observed findings when the participants were free to move their eyes. The stronger effects on pupil size in the absence of eye movement suggests that when the eyes were allowed to fixate, the individual elements, the fovea, and its immediate surrounding may have been selectively stimulated by these dark regions, which would have caused the eye pupil to slightly dilate. Moreover, increased eye movements in the first experiment during the light of cubes illusion, compared with the other illusions, could explain why the illusion initially failed to reveal significant differences, but

significantly smaller pupils were observed in the subsequent experiment when the eye did not change position.

It is clear from both experiments that pupillary constrictions to illusions can occur remarkably fast, and constrictions already peaked at ~150–200 ms from the onset of the image; in addition, pupillary constrictions could still be expressed 2–4 s after onset in some cases. Note also that the pupils (Fig. 3), though initially constricting in all cases, would eventually express dilations at different time points. Based on our previous assumption that the task of sustaining attention for several seconds would result in a gradual, slow dilation of the pupil (29, 31), we would also expect that such an opposing process would be more rapidly expressed for the weakest illusions (e.g., the Kanisza pictures).

Thus, our main conclusion is that the pupillary responses are rapidly matched to our subjective perception of light intensity, and the pupil slowly adapts to the actual physical intensity of the light. In other words, the pupils reflect almost instantaneously what we think we see. We surmise that such a pupillary response is the outcome of visual feedback information that is derived top-down, from the higher-level cortical areas to the low-level sub-cortical areas that control the pupillary light reflex. The clinical observations that patients whose visual cortex was damaged and who lost conscious visual perception continued to show adjustment of the pupils to changes in illumination (4) would then suggest that the neural circuitry involved in the control of pupil size can act independently of cortical signals. However, the present effects of illusory lightness/brightness on pupillary responses also suggest that such a low-level neural control circuitry of pupil size normally receives fast, modulatory signals from higher-level areas that elaborate the percept.

The present pupillary effects in response to illusory lightness/brightness appear rather small compared with the effect of a physical light increases on the pupil, and one could be skeptical about its functional significance or strategic purpose. However, a preparatory movement would be clearly beneficial in nonillusory conditions that are likely to result in exposures to physically strong light sources or surfaces strongly reflecting light. In other words, the illusory lightness/brightness could represent a signal that a stimulus is a potentially likely sender of strong light energy. An example is given by the subjective experience of luster that one receives from the shiny surface of polished gold or silver. The

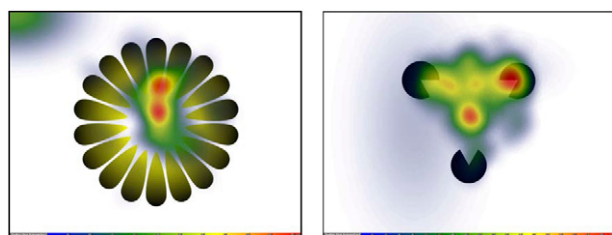


Fig. 5. Two examples of cumulative location of gaze, represented as heat maps (colors represent categorically increasing mean fixation times, from a minimum of 50 ms to a maximum of 562 ms; white represents no fixations in that region). Each image illustrates eye behavior of all participants of experiment 1 in one trial presentation of the Asahi illusion of brightness (Left) and of the Pacman illusion of lightness (Right).

perception of luster is due to retinal rivalry—that is, strong but local brightness differences can be detected with very small changes of viewing angle, so that the same silvery object actually looks lackluster to a single eye (33). The existence of a link between the perception and a protection reflex, such as the pupillary constriction against increasing illumination, suggests that these illusions, no different from other visual or optical illusions, represent a biological adaptation of our visual system (5–10, 34, 35).

Materials and Methods

Experiment 1. Fifteen students (nine females) of the University of Oslo volunteered for the experiment (mean age = 23.4; SD = 3.3). All participants had normal or corrected-to-normal visual acuity, and showed no signs of color vision deficiencies, as measured with the Ishihara plates. A remote eye-tracking device by SensoMotoric Instruments was used to record the horizontal and vertical coordinates of each participant's left eye. The eye tracker had a 2-ms sample rate with a resolution <0.1°; it operated with an infrared light-sensitive video camera that allowed recording in illuminated rooms. The illumination of the testing room was kept constant throughout testing sessions. The stimuli consisted of four illusions of brightness (Fig. 1). Each figure was presented in four different versions, presented twice and trials ($n = 32$) were randomly mixed.

All stimuli, when considered as whole images, were equiluminant. In particular, the various versions of the Kitaoka figures were obtained by displacing or translating over the background all of the original colored shape elements. Given that the Michelson contrast (C) is defined as $C = L_{\max} - L_{\min} / L_{\max} + L_{\min}$, the extreme luminance values can be displaced on the screen but the ratio of luminance change to mean background luminance remains constant. For the two Kanizsa figures, given that the addition of extra lines and forms increases the number of black pixels and therefore decreases luminance, brightness was controlled by changing the size of the inducing shapes so that the mean luminance of each picture also remained constant. Each target image was presented for 4 s. Before each image a gray screen or blank screen that was equiluminant to the subsequent target image was

presented for 500 ms; recordings during blank presentations were used as baseline measurement for the immediately subsequent target image. No explicit response (verbal or key press) was required during the viewing of the stimuli.

After removing eye-blink artifacts, a single measure of pupil diameter was obtained for each sample by averaging the horizontal and vertical coordinates of the pupillary diameter. Then, for each participant, we determined the average pupillary diameter recorded during each baseline presentation and each subsequent image. A filtering procedure was also used to remove measurements of the pupil that were >9 mm or <2 mm (i.e., beyond the physiologically normal range of pupillary diameters) as well as all low-frequency peaks that were >3 SDs from the mean pupil value. The data were then resampled in time bins of 10 ms each. The average for the baseline condition was then subtracted from the pupillary diameters recorded for the corresponding visual form's image. The obtained baseline-corrected data on mean change in pupillary diameters for the whole 4-s period were then entered in four separate repeated-measures ANOVAs (one for each figure type: Asahi, light of cubes, Kanizsa, and Pacman) with picture (A, B, C, and D) as the within-subject factors.

Experiment 2. Seventeen students (11 females) of the University of Oslo volunteered for the experiment (mean age = 24.5; SD = 2.9). Only those two versions of each illusion that in the previous experiment had produced maximum and minimum pupillary dilation were presented. Pupillary were recorded for the equiluminant baseline images and pictures for the first 300 ms from each illusion's onset. Two control stimulus conditions were added for one of the Kanizsa illusions (i.e., Pacman). Each of the 10 pictures was presented 10× and all trials ($n = 100$) were randomly mixed. In a separate session, each variant within each class of illusion images was presented 10× paired to another variant, side by side, on the same screen and at the same size of the eye-tracking session, and it was rated in terms of relative lightness/brightness. This procedure establishes a relative probabilistic psychophysics function for each comparison.

- Loewenfeld I (1993) *The Pupil: Anatomy, Physiology, and Clinical Applications* (Wayne State Univ Press, Detroit).
- Aston-Jones G, Cohen JD (2005) An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annu Rev Neurosci* 28: 403–450.
- Barbur JL (2004) *The Visual Neurosciences*, eds Chalupa LM, Werner JS (MIT Press, Cambridge, MA).
- Brindley GS, Gautier-Smith PC, Lewin W (1969) Cortical blindness and the functions of the nongeniculate fibres of the optic tracts. *J Neurol Neurosurg Psychiatry* 88: 259–264.
- Kanizsa G (1976) Subjective contours. *Sci Am* 234:48–52.
- Kanizsa G (1979) *Organisation in Vision* (Praeger, New York).
- Kitaoka A (2005) *Trick Eyes* (Barnes & Noble, New Providence, NJ).
- Hoffman DD (1998) *Visual Intelligence* (Norton, New York).
- Purves D, Lotto RB (2011) *Why We See What We Do Redux: A Wholly Empirical Theory of Vision* (Sinauer, Sunderland).
- Purves D, Wojtach WT, Lotto RB (2011) Understanding vision in wholly empirical terms. *Proc Natl Acad Sci USA* 108(Suppl 3):15588–15595.
- Slooter, van Norren D (1980) Visual acuity measured with pupil responses to checkerboard stimuli. *Invest Ophthalmol Vis Sci* 19:105–108.
- Drew P, Sayres R, Watanabe K, Shimojo S (2001) Pupillary response to chromatic flicker. *Exp Brain Res* 136:256–262.
- Li Z, Sun F (2005) Pupillary response induced by stereoscopic stimuli. *Exp Brain Res* 160:394–397.
- Kahneman D, Beatty J (1966) Pupil diameter and load on memory. *Science* 154: 1583–1585.
- Laeng B, Ørbo M, Holmlund T, Miozzo M (2011) Pupillary Stroop effects. *Cogn Process* 12:13–21.
- Einhäuser W, Stout J, Koch C, Carter O (2008) Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proc Natl Acad Sci USA* 105:1704–1709.
- Thorpe SJ, Fize D, Marlot C (1996) Speed of processing in the human visual system. *Nature* 381:520–522.
- Vogels R (1999) Categorization of complex visual images by rhesus monkeys. Part 2: Single-cell study. *Eur J Neurosci* 11:1239–1255.
- Perrett DI, Rolls ET, Caan W (1982) Visual neurones responsive to faces in the monkey temporal cortex. *Exp Brain Res* 47:329–342.
- Oram MW, Perrett DI (1992) Time course of neural responses discriminating different views of the face and head. *J Neurophysiol* 68:70–84.
- Altmann GTM (2011) Language can mediate eye movement control within 100 milliseconds, regardless of whether there is anything to move the eyes to. *Acta Psychol (Amst)* 137:190–200.
- MacEvoy SP, Paradiso MA (2001) Lightness constancy in primary visual cortex. *Proc Natl Acad Sci USA* 98:8827–8831.
- Roe AW, Lu HD, Hung CP (2005) Cortical processing of a brightness illusion. *Proc Natl Acad Sci USA* 102:3869–3874.
- Huang X, MacEvoy SP, Paradiso MA (2002) Perception of brightness and brightness illusions in the macaque monkey. *J Neurosci* 22:9618–9625.
- Kardon RH, Kirkali PA, Thompson HS (1991) Automated pupil perimetry. Pupil field mapping in patients and normal subjects. *Ophthalmology* 98:485–495, discussion 495–496.
- Clarke RJ, Zhang H, Gamlin PDR (2003) Characteristics of the pupillary light reflex in the alert rhesus monkey. *J Neurophysiol* 89:3179–3189.
- Beatty J, Lucero-Wagoner B (2000) *Handbook of Psychophysiology*, eds Cacioppo JT, Tassinary LG, Berntson GC (Cambridge Univ Press, Cambridge, UK).
- Kahneman D (1973) *Attention and Effort* (Prentice-Hall, Englewood Cliffs, NJ).
- Beatty J (1982) Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychol Bull* 91:276–292.
- Paulsen HG, Laeng B (2006) Pupillometry of grapheme-color synaesthesia. *Cortex* 42: 290–294.
- Laeng B, Sirois S, Gredebäck G (2012) Pupillometry: A window to the preconscious? *Perspect Psychol Sci* 7:18–27.
- Weiskrantz L, Cowey A, Barbur JL (1999) Differential pupillary constriction and awareness in the absence of striate cortex. *Brain* 122:1533–1538.
- Gregory RL (2009) *Seeing Through Illusions* (Oxford Univ Press, Oxford).
- Spillmann L, Dresch B (1995) Phenomena of illusory form: Can we bridge the gap between levels of explanation? *Perception* 24:1333–1364.
- Changizi MA, Hsieh A, Nijhawan R, Kanai R, Shimojo S (2008) Perceiving the present and a systematization of illusions. *Cogn Sci* 32:459–503.