Afterimage size is modulated by size-contrast illusions

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Traditionally, the perceived size of negative afterimages has been examined in relation to E. Emmert’s law (1881), a size–distance equation that states that changes in perceived size of an afterimage are a function of the distance of the surface on which it is projected. Here, we present evidence that the size of an afterimage is also modulated by its surrounding context. We employed a new version of the Ebbinghaus–Titchener illusion with flickering surrounding stimuli and a static inner target that generated a vivid afterimage of the latter but not the former. Observers were asked to give an initial manual estimate of the size of the inner target during the adaptation phase followed by another manual estimate of the size of the afterimage during the test phase. Manual estimates were affected by the size-contrast illusion both when the surrounding contextual elements were present during afterimage induction and when the surrounding elements were absent during the viewing of the afterimage (Experiment 1). Such a modulation in perceived size, however, did not occur when observers viewed only the flickering surrounding context for a prolonged period of time and then estimated the size of a static target presented on the monitor afterward, demonstrating that flickering stimuli by themselves did not produce any aftereffect on perceived size (Experiment 2). Furthermore, in a final experiment, we showed that the modulation observed in the test phase of Experiment 1 was not due to memory of the manual estimates that had been performed during the adaptation phase (Experiment 3). These findings provide clear evidence for the role of high-level cognitive processes on the perceived size of an afterimage beyond the retinal level. Thus, although retinal stimulation is required to induce an afterimage, post-retinal factors influence its perceived size.

Keywords: afterimage, Ebbinghaus–Titchener illusion, perceived size


Introduction

Adaptation to a chromatic surface generates negative afterimages, which have brightness and color complementary to the original pattern (Kelly & Martinez-Uriegas, 1993). Afterimages have long been studied in relation to Emmert’s law (Emmert, 1881) to explain size constancy, which is the perceptual ability to make accurate size judgments of objects placed at different distances from the eyes (e.g., Holway & Boring, 1941; Ross & Plug, 1998; Sperandio, Savazzi, Gregory, & Marzi, 2009). Unlike images of external objects, afterimages are unchanging stimuli fixed to the retina and like shadows can be “projected” upon a wall or surface at different viewing distances. Of course, the retinal size of an afterimage stays the same regardless of where it is seen. Nevertheless, the greater the viewing distance, the larger the afterimage appears to be. This simple demonstration shows that the perceived size of an object depends on its perceived distance multiplied by the retinal angle subtended, as formally postulated by Emmert more than a century ago (for further discussion, see Edwards & Boring, 1951; Gregory, 2008; Hastorf & Kennedy, 1957; Lou, 2007; Weintraub & Gardner, 1970).

Emmert’s law is a convincing demonstration that the apparent size of an object is not a simple function of the size of its retinal image but also depends on the perception of its distance. By the same token, Emmert’s law implies that any misperception of distance will involve a misperception of size and vice versa. Thus, an afterimage appears larger on an illusorily farther surface (Dwyer, Ashton, & Boerse, 1990), such as the far wall of an Ames Room (i.e., distorted room). Furthermore, it has been shown that an afterimage will change shape when viewed on an apparently tilted surface (Boerse, Ashton, & Shaw, 1992). All of this demonstrates that errors in depth perception, including those arising from top-down processing, can sometimes lead to errors in size judgments (Gregory, 2008).

In fact, there are many examples of situations in which the perceived size of a visual stimulus can be affected by
the context in which it is viewed. The Ebbinghaus or Titchener circles illusion, in which a target disk surrounded by small circles appears to be larger than an identical disk surrounded by large circles, is one example of such a situation (Figure 1a). Visual illusions such as the Ebbinghaus–Titchener illusion are called size-contrast illusions since the size of the stimulus target is perceived relative to the inducing elements (or surrounding context) and appears to grow or shrink depending on the size of these inducers (e.g., Coren & Enns, 1993).

O’Halloran and Weintraub (1977) showed that photo-flash-generated afterimages of the surrounding context of the Delboeuf illusion (i.e., a size-contrast illusion) can generate an underestimation of the size of an outline test circle, indicating that afterimages can affect the perceived size of a physically presented object. It is possible, however, that retinal factors, such as lateral inhibition (Ganz, 1966a, 1966b), might have contributed to the size-contrast illusion, given that an afterimage of surrounding context as well as the target was simultaneously presented on the retina during the perceptual judgment task in O’Halloran and Weintraub’s study. To rule out this possibility and to explore the role that higher order visual processing might play in the generation of afterimages, we designed an experiment in which the observer was presented with a different version of the Ebbinghaus–Titchener illusion with flickering surrounding stimuli and a static inner inducer. Counterphase-flickering stimuli do not generate a detectable afterimage because the processes underlying the generation of the negative afterimage are too slow to follow the local changes in luminance of the flickering stimuli—and thus, no polarity-specific adaptation occurs following prolonged exposure to such flickering stimuli (Burbeck, 1986). Therefore, an illusory display that contains a flickering surrounding context should result in an afterimage of only the static target. Any modulation in perceived size of this afterimage would depend on post-retinal factors, since not only were the surrounding stimuli no longer present on the retina but even during the induction phase these flickering stimuli would not have generated persistent lateral inhibition.

**Experiment 1: Ebbinghaus–Titchener illusion with flickering circles**

The purpose of this experiment was to study the effects of size-contrast illusions on perceived afterimage size. A target surrounded by small or big flickering surrounding stimuli (which do not create an afterimage themselves) should result in an afterimage that observers will perceive bigger or smaller, respectively, despite having the same retinal size.

**Methods**

**Observers**

Six volunteers (4 males), ranging in age from 18 to 26 years with normal or corrected-to-normal vision, took
part in the experiment. Observers received one course credit for their participation and written consent was obtained prior to testing.

**Apparatus**

The stimuli and the psychophysical experiments were programmed in E-Prime (Psychology Software Tools, Pittsburgh, PA) on a Dell Pws670, running Windows XP. Images were displayed on a 19-inch RGB color monitor, with $1024 \times 768$ pixel resolution at 60-Hz frame rate. Observers were seated in front of the computer monitor in a dark room and viewed displays binocularly with their chin and forehead fixed on a chin rest. The viewing distance was 57 cm.

**Experimental design**

Observers could initiate the experiment by pressing the space bar of the PC keyboard. Each trial was composed of two phases:

1. **Adaptation phase**: The stimulus used to generate the afterimage was a dark red circle (luminance = 4.2 cd/m²) presented in the center of the screen on a gray background (luminance = 6.9 cd/m²) with an exposure duration of 30 s. The diameter of the circle was 3.2° in visual angle and it was surrounded by an annulus of six flickering circles. Each surrounding circle was made up of small squares that flickered between four different shades of gray (from dark to light gray) at a rate of 4 Hz with an average luminance of 5.9 cd/m². In the “Large flickering annulus” condition, the diameter of each of the peripheral circles was 4.7° in visual angle. In the “Small flickering annulus” condition, the diameter of each of the peripheral circles was 1.5° in visual angle. Annuli were arranged around the fixation point in a way that their centers were located on the corners of an imaginary hexagon, and as a result, their distances from the fixation point were the same (Figure 1a). The distance between fixation point and internal borders of the peripheral circles was equal in both “Large flickering annulus” and “Small flickering annulus” conditions (3° in visual angle). Observers were instructed to maintain fixation on a small black dot presented in the center of the static circle and indicate the perceived diameter of the target circle by adjusting the aperture between their thumb and index finger. These manual estimates were then measured in mm with a ruler. Observers were required to use their right hand and rest it on the table when making the manual estimate. This kind of magnitude estimation method has been used in previous studies to examine the effect of size-contrast illusions on visual perception (e.g., Haffenden & Goodale, 1998; Westwood & Goodale, 2003). The entire display disappeared at the end of the adaptation phase.

2. **Test phase**: In the test phase, the display was replaced by a uniform gray background with a fixation point in the middle (Figure 1b). Observers were asked to keep their gaze on the fixation point and as soon as they perceived the afterimage to indicate its diameter by adjusting the aperture between their thumb and index finger without looking at their hand. Observers were also invited to wait until the afterimage had completely disappeared before initiating a new trial.

The experiment was divided into two blocks of 10 trials (5 large circle annulus trials and 5 small circle annulus trials). “Large flickering annulus” and “Small flickering annulus” conditions followed a randomized order. Observers were given two practice trials before testing began.

**Results and discussion**

Observers never reported any afterimage of the surrounding circles, indicating that only afterimages of the central inducing stimulus were generated by the illusory display during the adaptation phase. The afterimage of the inducer persisted for approximately 10 s. Figure 2 shows mean perceived diameter of the static target and the afterimage for the two display conditions. A two-way analysis of variance (ANOVA) was carried out on manual estimates with Phase (adaptation versus test) and Display (small flickering annulus versus big flickering annulus) as main factors. The main effect of Phase was significant ($F_{(1,5)} = 14.194, p = 0.013$) as was the main effect of Display ($F_{(1,5)} = 24.268, p = 0.004$), but their interaction was not ($F_{(1,5)} = 0.635, p = 0.462$). The magnitude of the illusion as measured by the manual estimation task was 7.7% for the static target and 6.3% for its afterimage. These values are compatible with the range of 5–10% found on average (McCready, 1985; Rose & Bressan, 2002). Overall, an afterimage was perceived 9.7% smaller than its original stimulus possibly reflecting differences in luminance contrast between the adaptation and test phases (Weintraub, Tong, & Smith, 1973). Results from this experiment demonstrate that the apparent size of an afterimage is modulated by size-contrast illusions even when surrounding elements are no longer present on the retina. Moreover, the fact that the illusion operated with a flickering surround strongly suggests that lateral inhibition operating at the level of the retina was not the primary mechanism underlying the illusion.

**Experiment 2: Do flickering circles induce an aftereffect?**

Experiment 1 demonstrated that perceived size of an afterimage can be affected by the Ebbinghaus–Titchener illusion even if the surrounding context was no longer present during the afterimage perception. To rule out the possibility that this modulation was in fact a consequence of an aftereffect generated by the flickering surrounding...
context, we performed a second experiment in which observers estimated the perceived size of a static circle that was presented after prolonged period of adaptation with flickering stimuli. If flickering circles induced an aftereffect, then the perceived size of the target circle should be prone to the size-contrast illusion as a result of mutual inhibition effects between target and the context contours of any afterimage that might be present. We also included a condition in which we presented non-flickering (static) annuli during the adaptation phase to make sure that an afterimage of a surrounding annulus would indeed induce a size-contrast illusion.

**Methods**

**Observers**

Six volunteers (2 males), ranging in age from 18 to 25 years with normal or corrected-to-normal vision, took part in the experiment. Observers received monetary compensation for their participation and written consent was obtained from all observers prior to testing.

**Apparatus**

The same equipment and setup that were used in Experiment 1 were used here.

**Experimental design**

Observers could initiate the experiment by pressing the space bar of the PC keyboard. Each trial was composed of two phases:

1. Adaptation phase: Annuli of six flickering or static circles (see Methods section of Experiment 1) were presented in the center of the screen on a gray background (luminance = 6.9 cd/m²) with an exposure duration of 30 s (Figure 3a). Observers were instructed to maintain fixation on a small black dot presented in the middle of the screen. The entire display disappeared at the end of the adaptation phase.

2. Test phase: In the test phase, the flickering or the static display was replaced by a static light green circle (luminance = 12.7 cd/m²) on a uniform gray background with a fixation point in the middle (Figure 3b). The diameter of the circle was 3.2° in visual angle. Observers were instructed to keep their gaze on the fixation point and give a manual estimate of the perceived diameter of the circle by adjusting the aperture between their thumb and index finger (see Methods section of Experiment 1). The target circle was presented for 5 s.

The experiment was divided into two blocks of 20 trials (10 large circle annulus trials and 10 small circle annulus trials). The presentation of flickering and static displays was counterbalanced across subjects while the size of the annulus (small vs. large) followed a randomized order. Observers were given two practice trials before testing began.

**Results and discussion**

A two-way analysis of variance (ANOVA) was carried out on the manual estimates with Display (flickering versus...
static) and Size (small annulus versus large annulus) as main factors. Figure 4 shows mean perceived target size for each stimulus condition. The main effect of Size was significant ($F_{(1,5)} = 11.758$, $p = 0.019$) while the main effect of Display was not ($F_{(1,5)} = 2.705$, $p = 0.161$). More importantly, their interaction reached significance ($F_{(1,5)} = 19.243$, $p = 0.007$). Post hoc $T$ test with Bonferroni correction showed that the only significant comparison ($T_5 = 4.085$, $p = 0.009$) was between “Small static annulus” (3.89 cm) and “Large static annulus” (3.48 cm) conditions. The magnitude of the illusion as measured by the manual estimation task was 11.8%. No difference was observed in the perceived size of the inner target when a small or large flickering display had been previously presented. This result indicates that the perceived size of the target circle was not affected by prior presentation of

Figure 3. Experiment 2. (a) During the adaptation phase, an annulus of big circles (“Large flickering or static annulus”) or small circles (“Small flickering or static annulus”) was presented for 30 s. (b) A static circle was presented on a uniform background. No afterimages of the flickering circles were generated.

Figure 4. The results of Experiment 2. Mean perceived diameter in cm of the static circle as a function of surrounding annulus size. Note that in the test phase an afterimages of the static, but not of the flickering, surrounding context was generated. Error bars in the figure indicate the within-subject 95% confidence interval (Loftus & Masson, 1994) based on the error term from a one-way ANOVA with 4 levels.
flickering annuli with different circle sizes, supporting the hypothesis that flickering stimuli do not generate appreciable afterimages. In contrast, when the same surrounding context was not flickering, the earlier presentation of annuli with different circle sizes had an effect on the perceived size of the test circle.

**Experiment 3: Does memory affect manual estimates?**

To ensure that results in Experiment 1 were not contaminated by a memory effect on the manual estimates, in this final experiment we employed a complete flickering version of the Ebbinghaus–Titchener illusion. As discussed earlier, if a display contains flickering stimuli, then no afterimages should occur. The experimental setting was identical to that of Experiments 1 and 2 except that the apparent size of a flickering inner target was indicated by our observers during and after the presentation of the surrounding elements that were also flickering. If the observers in Experiment 1 had simply remembered the size of the manual estimates they had given in the adaptation phase and reproduced them in the test phase, then in Experiment 3 they should also show a similar pattern of responding in the adaptation and test phases, i.e., they should open their hand wider for the flickering stimulus that had earlier been surrounded by a small flickering annulus and smaller for the stimulus that had been surrounded by a large flickering annulus. However, if the effect in Experiment 1 was due to a change in the central representation of the afterimage, then there should be no carryover from the adaptation phase to the test phase in Experiment 3.

**Methods**

**Observers**

Six volunteers (3 males), ranging in age from 18 to 32 years with normal or corrected-to-normal vision, took part in the experiment. Observers received monetary compensation for their participation and written consent was obtained from all observers prior to testing.

**Apparatus**

The same equipment and setup that were used in Experiments 1 and 2 were used here.

**Experimental design**

Observers could initiate the experiment by pressing the space bar of a keyboard. Each trial was composed of two phases:

1. Adaptation phase: A flickering version of the Ebbinghaus–Titchener illusion (see Methods section of Experiment 1) was presented in the center of the screen on a gray background (luminance = 6.9 cd/m²)

![Figure 5.](image)

**Figure 5. Experiment 3.** (a) A flickering version of the Ebbinghaus–Titchener illusion was presented for 30 s during the adaptation phase. (b) The inner flickering circle was displayed alone on the screen during the test phase.
with an exposure duration of 30 s (Figure 5a). Observers were instructed to maintain fixation on a small black dot presented in the middle of the inner flickering target and give a manual estimate of the perceived diameter of the circle by adjusting the aperture between their thumb and index finger (see Methods section of Experiment 1). The entire display disappeared at the end of the adaptation phase.

2. Test phase: In the test phase, the flickering surrounding annulus was removed and only the inner flickering target with a fixation point in the middle was displayed for 5 s (Figure 5b). Observers were asked to keep their gaze on the fixation point and indicate perceived target diameter by adjusting the aperture between their thumb and index finger.

The experiment was divided into two blocks of 10 trials (5 large circle annulus trials and 5 small circle annulus trials). “Large flickering annulus” and “Small flickering annulus” conditions followed a randomized order. Observers were given two practice trials before testing began.

Results and discussion

Figure 6 shows mean perceived diameter of the flickering target for the two display conditions during adaptation and test phases. A two-way analysis of variance (ANOVA) was carried out on manual estimates with Phase (adaptation versus test) and Display (small flickering annulus versus large flickering annulus) as main factors. The main effect of Display was significant ($F_{(1,5)} = 17.734, p = 0.008$), while the main effect of Phase was not ($F_{(1,5)} = 1.164, p = 0.330$). More importantly, their interaction was significant ($F_{(1,5)} = 125.032, p < 0.001$). Post hoc T test with Bonferroni correction showed that the only significant comparison ($T_5 = 6.471, p = 0.001$) was between small (4.85 cm) and large (4.43 cm) flickering annuli during the adaptation phase. No difference was observed for manual estimation of size of the target during the test phase as a function of the size of the surrounding context previously presented during the adaptation phase. This interaction is important because it demonstrates that the illusion had an effect on the perceived target size only when the Ebbinghaus–Titchener illusion was displayed, indicating that observers were not using their memory of what they had done (or seen) in the adaptation phase to influence their manual estimates in the test phase, when the flickering annulus was no longer present. Importantly, this result makes it clear that a memory-based account cannot explain the effects observed in Experiment 1. In addition, the absence of any differences in manual estimates as a function of earlier exposure to a flickering display further confirms the finding that flickering stimuli do not generate aftereffects.

General discussion

The general finding emerging from the present study is that the perceived size of an afterimage is affected by
size-contrast illusions when the surrounding contextual elements were present during the induction of the afterimage but not later when the afterimage was being viewed. In Experiment 1, we found that size judgments of the static target and its subsequent negative afterimage were modulated by the surrounding context that was present during the adaptation phase. It seems reasonable therefore to argue that the perception of afterimages and the perception of real objects share similar mechanisms for computing size, given that both are affected by size-contrast illusions in the same way. This is in keeping with the idea of a common neural correlate of visual consciousness for images and afterimages (Kirschfeld, 1999).

Importantly, our results cannot be explained by suggesting that aftereffects were induced by the flickering surrounding context (Experiment 2) or were due to memory effects that were carried over from the adaptation phase to the test phase (Experiment 3). The demonstration that flickering contextual information modulated the apparent size of negative afterimages but not the apparent size of physical stimuli in the test phase (when no contextual information was present) strongly suggests that a persistent aftereffect of lateral inhibition operating at the level of the retina during the adaptation phase did not play a role in the later illusory effects observed with the afterimage in Experiment 1. It has been shown (Fiorentini & Maffei, 1970; Kelly, 1969) that flickering stimuli, especially below 10 Hz, generate a pattern effect that can be explained in terms of temporal characteristics of excitation and inhibition. In other words, it is unlikely that the flickering surrounding context we presented would have generated a persistent lateral inhibition but rather an alternation of excitation and inhibition. In short, the strength of lateral inhibition for flickering stimuli would have been considerably reduced. At a more general level, such a finding argues against the idea that lateral inhibition at the level of the retina plays a prominent role in size-contrast illusions such as the Ebbinghaus–Tichener illusion. Of course, this is not to say that such effects might not operate centrally at the level of the cerebral cortex.

What neural mechanisms are responsible for the perception of afterimages? Although afterimages have been studied for a long time, there is still no consensus about their origin. A broad range of evidence indicates that afterimages have a retinal locus (e.g., Brindley, 1962; MacLeod & Hayhoe, 1974; Rushton & Henry, 1968; Williams & MacLeod, 1979). It has been reported that an afterimage can be generated even when the inducing stimulus has never been perceived because of pressure blinding applied to the sclera (Craik, 1940) and that negative afterimages do not show interocular transfer (von Wright, 1963). These observations are in agreement with the assumption that afterimages are primarily retinal. Nevertheless, adaptation of photoreceptors at the retinal level cannot fully explain this complex phenomenon.

Shimojo, Kamitani, and Nishida (2001), for example, examined adaptation to color spreading in an illusory-contour figure. They obtained different kinds of afterimages as a result of adaptation to either the contour of the inducers (a local afterimage) or the perceptually filled-in surface (a global afterimage). In other words, they found that fixating color-spreading configurations produced afterimages that required adaptation that was mediated by a cortical representation of visual information. Similarly, van Lier, Vergeer, and Anstis (2009) suggested that an afterimage can be modulated by cortical filling-in processes. The authors reported that afterimage colors could spread across previously uncolored areas and that perceived color and shape of the afterimage could be triggered and constrained by the shape of a subsequent contour. Further evidence in favor of a cortical role in the perception of afterimages comes from studies on the effects of visual attention on the perceived duration of negative afterimages (Lak, 2008; Suzuki & Grabowecky, 2003). Results from these experiments showed that an afterimage was weaker when observers attended to the inducer during adaptation than when subject’s attention was engaged away from it by means of an attentional task. More recently, van Boxtel, Tsuchiya and Koch (2010) reported opposite effects of attention and awareness (visibility of the inducer) on afterimage duration: Paying attention to the inducer reduces afterimage duration, whereas enhancing awareness of the inducer increases afterimage duration.

It is well known that filling in, attention, and awareness are all processes that depend on higher cognitive functions. Taken together, these findings lead to the conclusion that the perception of afterimages is not a simple consequence of bleaching photoreceptor pigments in the retina but also depends on mechanisms operating at much higher levels of processing in the brain. Our demonstration that the perceived size of a negative afterimage is affected by the presence of contextual elements during the adaptation phase is consistent with this hypothesis.

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