

Pupil dilation to illusory motion in peripheral drift images: Perception versus reality

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Peripheral drift is a specific type of illusory motion that causes observers to perceive motion in a static image. We aimed to determine whether pupil dilation occurs during the perception of illusory motion. In three experiments investigating pupil-size changes to peripheral drift, pupil response differences were observed between symmetric patterns (SPs) that elicited no impression of motion and repeated asymmetric patterns (RAPs) that did. All participants reported the perception of motion in the RAP condition and showed significantly greater pupil dilation to these stimuli as compared with viewing stimuli in the SP condition. As a follow-up, we manipulated the RAP stimuli to reduce and then remove the illusion to determine (a) whether it was the asymmetry per se that induced the pupil dilation and (b) whether the amount of pupil dilation was contingent on the amount of observed illusory motion. Although a reduction in perceived illusory motion did not produce a reduction in pupil dilation, removal of the illusory motion did. Despite previous evidence reporting pupil constriction to the perception of motion, and the positive valence associated with symmetry, these experiments show that pupil dilation occurs during the perception of illusory motion. This is in keeping with previous evidence that pupil dilation is influenced by perceptual factors and not simply light level, and, in particular, shows that illusory motion is physiologically arousing.

Introduction

Pupillometry is a measure of pupil diameter used in psychology and vision science to understand how pupil size corresponds to stimulation. Similar to a camera, changes in illumination and focus affect pupil size, with the pupil getting larger (dilating) to accommodate more light, and smaller (constricting) to focus on fine details or to accommodate less light (Ellis, 1981; Ripps, Chin, Siegel, & Breinin, 1962).

Although the low-level pupil reflex in response to changes in light level, known as the pupillary light response (PLR), is well-established, evidence has implicated a cognitive component to changes in pupil size (Beatty & Lucero-Wagoner, 2000; Loewenfeld, 1958). For example, demanding tasks such as recalling a long string of digits, solving a complicated math problem, or detecting continuity errors, all result in pupil dilation (Klingner, Tversky, & Hanrahan, 2011). Furthermore, pupil size has been shown to change when viewing a motion-induced blindness illusion in which a physically present stimulus appears and disappears, with pupil dilation observed during the reported disappearances (Kloosterman et al., 2015). Together, these studies demonstrate that components of cognitive processing, such as cognitive load, perceptual content, or surprise, have a direct effect on pupil size.

Even with regards to the seemingly involuntary PLR, the mechanism is not as straightforward as one might expect from a low-level reflex. As evidenced from several studies, a “simulated” PLR can be evoked without perceiving actual changes in light level, for

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example, through awareness, interpretation, and mental imagery. In the case of awareness, when images of different luminance are presented to each eye in a binocular rivalry experiment, both pupils constrict when the higher luminance image dominates perception, demonstrating that physical luminance alone is not sufficient to produce pupil changes (Naber, Frässle, & Einhäuser, 2011). Regarding interpretation, an image of the sun elicits a stronger PLR than other types of images with the same brightness, demonstrating the effect of prior knowledge on pupil size (Binda, Pereverzeva, & Murray, 2013). Finally, with mental imagery, even imagining looking at a bright stimulus, or preparing to do so, causes the pupils to constrict (Laeng & Endestad, 2012; Mathôt, van der Linden, Jonathan, & Vitu, 2014). These findings further demonstrate that the pupil is sensitive to higher-order cognition, and that changes in pupil size are not based simply on the physical stimulus.

Although the studies aforementioned highlight that higher-order perceptions and cognitions influence pupil size, they focus primarily on perceptual changes associated with changes in light level (Mathot & Van der Stigchel, 2015; Kloosterman et al., 2015). The goal of the current study is to determine whether similar pupil size changes occur during the presentation of a static stimulus that elicits illusory motion, that is, one outside the domain of conventional pupil reflexes. This can be accomplished using the peripheral drift motion illusion—a physically static image that provokes a strong sensation of motion; as observers move their eyes or blink rapidly, these images viewed peripherally appear to “drift” (hence the name; Faubert & Herbert, 1999; Fraser & Wilcox, 1979). A strong perception of illusory motion is experienced with a form of peripheral drift pattern termed a repeated asymmetric pattern, or RAP (Chi, Lee, Qu, & Wong, 2008), an example of which is shown in Figure 3.

Our prediction is that the perception of illusory motion will provoke pupillary dilation, and hence that pupil size will increase more when viewing the repeated asymmetric patterns (RAPs) than when viewing the symmetric patterns (SPs). Why? First, because pupil dilation is associated with perceptual content, and surprise (Hossain & Yeasin, 2014). In terms of perceptual content, illusory RAPs (Figure 3) are both physically static and perceptually dynamic whereas SPs (Figure 2) are physically and perceptually static. Second, visual illusions are inherently arousing. One study comparing the valence of visual illusions with their nonillusory counterparts found that on scales of aesthetic experience and arousal, participants rated illusions to be more pleasant and arousing than non-illusions (Stevanov, Marković, & Kitaoka, 2012). Notably, one illusion tested in their experiment was the famous rotating snakes illusion that uses RAPs to evoke the perception of illusory motion. Although this

study found no differences in the ratings specific to illusory motion versus controls, the authors recommended conducting a study employing a physiological measure that better reflected these affective changes in arousal—the exact purpose of this investigation.

Indeed, pupil size has been shown to be a useful indicator of physiological arousal, with direct connections to the locus coeruleus arousal network (Joshi, Li, Kalwani, & Gold, 2016). For example, both positive and negative pictures have been shown to elicit greater pupillary dilations than neutral pictures (Bradley, Miccoli, Escrig, & Lang, 2008). Importantly, this pattern of dilation covaried with skin conductance changes (as measured by the galvanic skin response), confirming pupillometry as a valid measurement for arousal mediated by the sympathetic nervous system. The data from these converging measures also seemed to indicate that pupillometry has the better temporal sensitivity, though this has yet to be thoroughly tested.

Our aim in using pupillometry to measure the response to illusory motion is to resolve conflicting predictions about motion and symmetry. Real coherent motion elicits pupil constriction (Sahraie & Barbur, 1997), so from this one might expect illusory motion to do the same, yet the surprise and arousal factor associated with illusory phenomena would lead one to expect pupil dilation not constriction. Secondly, a symmetric pattern, having positive valence and producing high arousal (Bertamini, Makin, & Rampone, 2013) and being a preferred pattern (Palmer, Schloss, & Sammartino, 2013), might be expected to elicit greater dilation than our RAPs.

We have therefore measured pupil size in response to peripheral drift illusions of various strengths as well as to symmetric patterns. We predict that the illusory RAPs will elicit a greater dilation than the nonillusory SPs, and that this difference will fade as a function of the decrease in RAP illusion intensity.

Methods

Experiment 1

Participants

Thirty-eight healthy volunteers affiliated with McGill University were recruited as observers. Three participants were excluded due to equipment fault. The remaining 35 participants ranged in age from 18 to 41 years old (median = 20 years; 20 females). All participants had normal or corrected-to-normal visual acuity, and did not possess any abnormalities of the eye. For all experiments included in this paper, participants gave informed consent prior to the study and the research protocol was approved by the McGill



Figure 1. Both patterns used in the SP and RAP conditions were created by systematically rotating and replicating this one local element.

University Ethics Committee. Furthermore, this research adhered to the tenets of the Declaration of Helsinki except for conditions intended for clinical trials including preregistration.

Equipment

Stimuli were generated within the MATLAB Psychophysics Toolbox 3.0 and were displayed on a 1,920- × 1,080-pixel ASUS PB238Q Professional Monitor, 23" Full-HD monitor (AsusTek Computer Inc., Taipei, Taiwan). The EyeTribe pupillometer was used to collect eye-gaze and pupil-size data via infrared reflections using the EyeTribe toolbox for MATLAB (version 0.0.3; Dalmaijer, 2014; Dalmaijer, Mathôt, & Van der Stigchel, 2013; The EyeTribe © 2016). The EyeTribe sampled pupil-size data at 60 Hz, collecting 540 data points per trial. Viewing distance to the monitor was 60 cm. Participants were placed in a chin and head rest to remove motion artifacts. Eye-gaze and fixation was calibrated prior to each experimental block.

Stimuli

Stimuli for this experiment were inspired from existing peripheral drift images (Backus & Oruç, 2005; Zanker, 2017) and were constructed such that the perception of illusory motion could be controlled through the physical orientation of local elements within the global pattern (Figure 1). Our stimuli

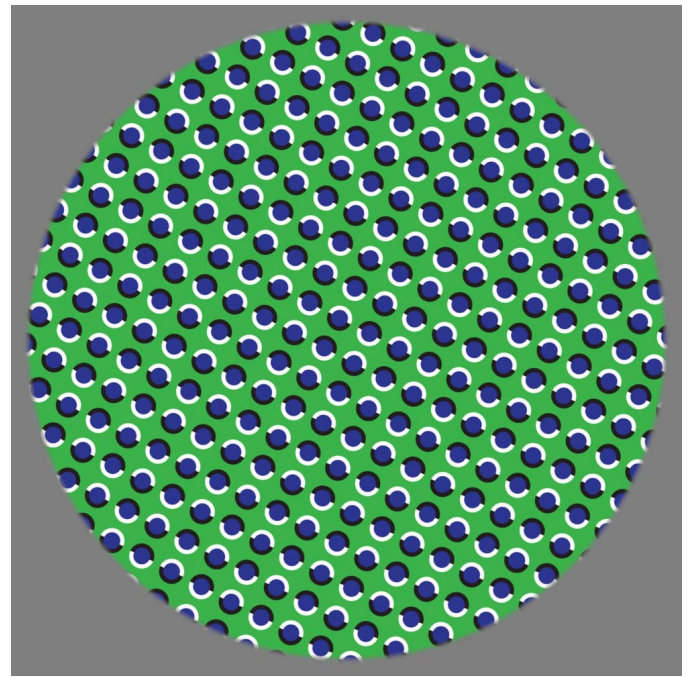


Figure 2. An example of one symmetric pattern (SP) created using the local element from Figure 1. Observers report no illusory motion in this pattern.

comprised three properties that elicited a strong perception of motion: (a) a repeating asymmetric pattern (RAPs; Chi et al., 2008), where local elements within the image are misaligned to create global asymmetry; (b) alternating black and white regions (Backus & Oruç, 2005; Zanker, Hermens, & Walker, 2010), where local elements contain neighboring contrasts of black and white (Fig. 1); and (c) color, which enhances the perception of the illusion. (Backus & Oruç, 2005; Chi et al., 2008; Kitaoka, 2014).

Prerequisites (a) and (b) aforementioned complement each other and are essential to the production of peripheral drift. That is, the orientation information provided by the specific positioning of the alternating black and white *creates* the repeated asymmetry within the global image (Figure 3), and subsequently creates illusory motion. Orienting the local elements within a column along the same rotational degree creates symmetric patterns (SPs) that destroy the illusion (Figure 2). Finally, color has been shown to enhance the perception of the peripheral drift, and specifically certain color pairs such as light-green and blue (Cheetham, Wu, Pauli, & Jancke, 2015). For this reason, these colors were used for our RAPs.

Creating the stimulus images in this way ensured control over several potentially confounding variables. First, because both illusory RAPs and nonillusory SPs are created from the same local element, the luminance properties in both conditions do not differ—an important consideration in pupillometry. Second, to alleviate

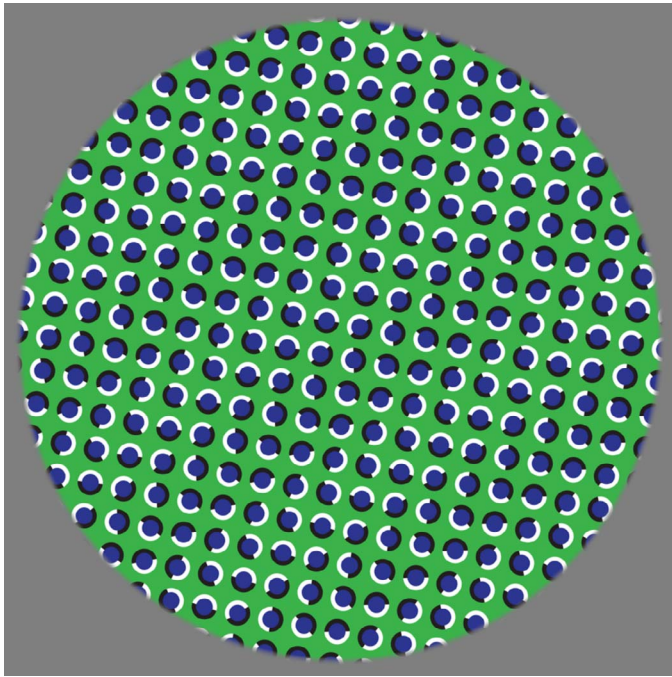


Figure 3. An example of one repeating asymmetric pattern (RAP) created using the local element from Figure 1. All observers reported seeing illusory motion. Recommended viewing conditions are bright high-definition monitors, or by following the details in the Methods section (viewing on printed paper not advised).

any effect on pupil size as a result of habituation, boredom, or fatigue, images in each condition were created by rotating all of the local elements the same degree to produce a unique pattern that adhered to the orientation rule (SP or RAP). Additionally, a random global rotation of the entire image was performed to change the perceived “direction” of the illusion. A circular aperture with a Gaussian blur was generated over the top of all images to help focus fixation and remove extraneous edge-information. All images were viewed from a visual angle of 25° ; images in all conditions were approximately 80 cd/m^2 .

Procedure and design

Demographic information about participants’ gender, age, ethnicity, handedness, eye color, vision correction, and illusion enjoyment were collected. Due to large variability in ability to perceive illusory motion (Backus & Oruç, 2005), participants were shown sample trials from both conditions prior to the experiment to ensure they could perceive the illusory motion. The actual experiment consisted of 50 images from each condition (100 total), broken up and randomly distributed into four 25-trial blocks to reduce dry eyes from visual fatigue. Each trial consisted of three phases: preparation (baseline), stimulus, and blink phases (Figure 4). The preparation phase served

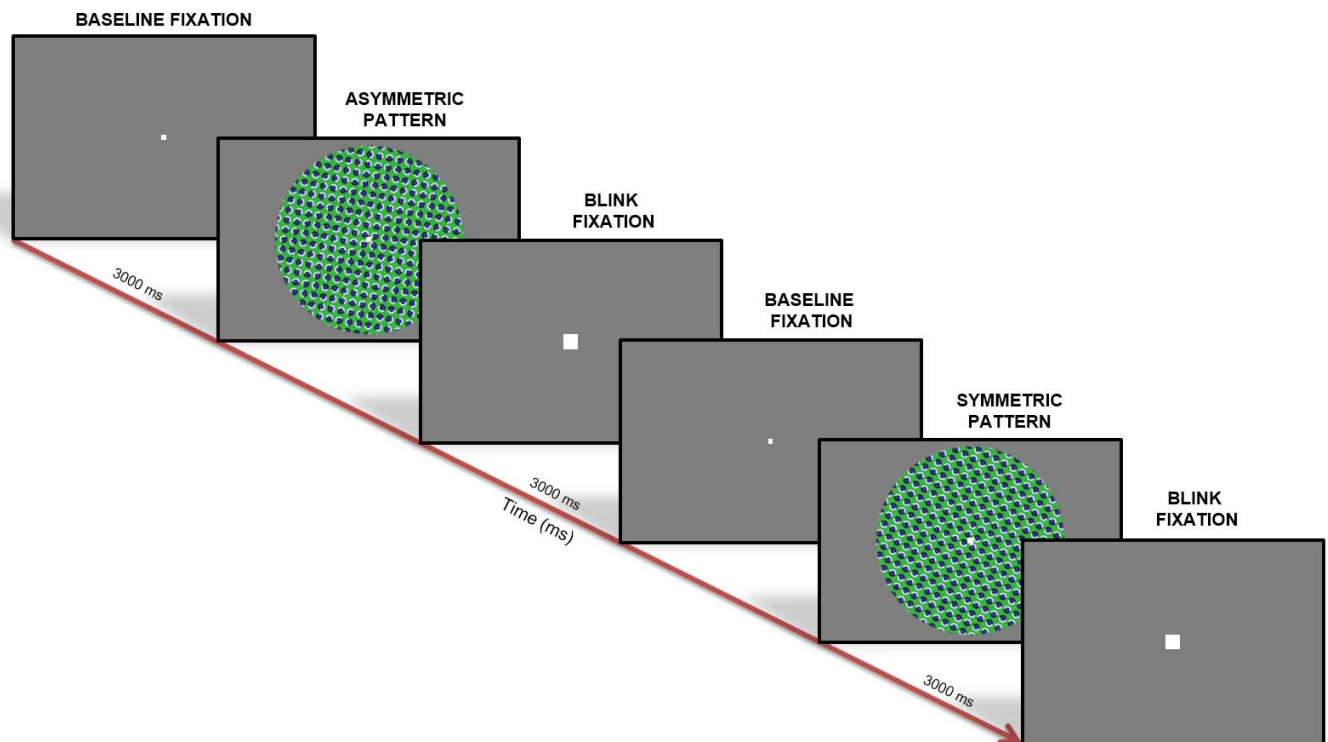


Figure 4. Experimental design. The three phases of a trial were the preparation (baseline) fixation, the stimulus phase (randomized asymmetric vs. symmetric conditions), and the blink fixation (3000 ms between each phase). Participants were instructed to fixate throughout the experiment, and to attempt to isolate any blinks to the blink fixation phase.

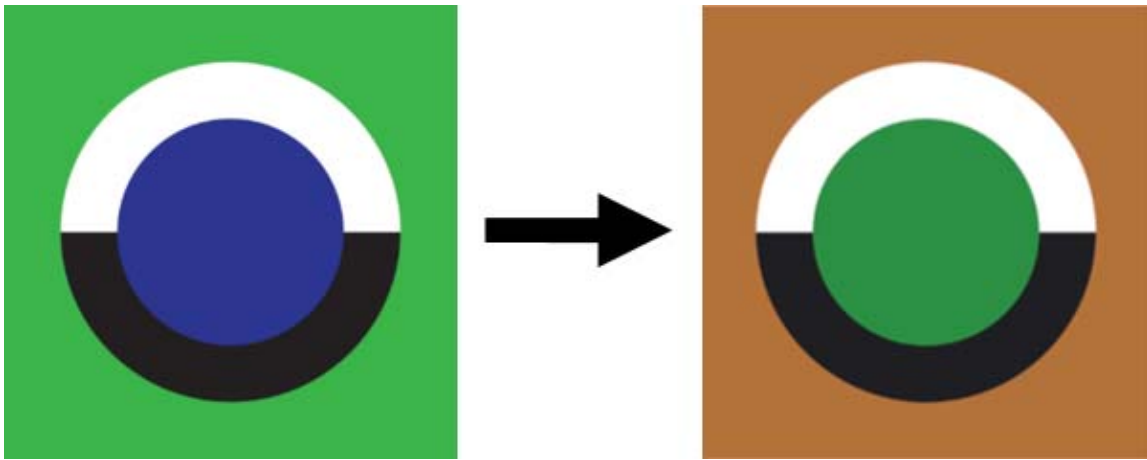


Figure 5. Stimulus hue adjustment. The images for the two conditions in Experiment 2 and 3 were created by mapping the hue of the local element from Experiment 1 onto a color wheel, and subtracting 100° from the overall image.

as a break from the bright stimulus to collect data for baseline correction. The phase of interest to the investigation is the stimulus phase during which pupillary differences were expected. Following this, participants were encouraged to blink a few times to reduce dry eyes, as blinks during the stimulus phase were discouraged in order to prevent blinks (data loss) during the stimulus phase.

All phases were three seconds in duration, for a trial length of 9 s, and a block length of 4 min. The phase

lengths were chosen in part to allow sufficient exposure duration to the stimulus so that the naturally occurring pupillary light reflex (PLR) could recover, and differences in the dilation profile could instead be attributed to the stimulus properties. Furthermore, the blink and the preparation phase (of the next trial) was sufficiently long to prevent the build-up of after-images. To avoid any effect of eye-movements on pupil-size, participants were asked to remain fixated on the center of the screen for the entire length of the experiment.

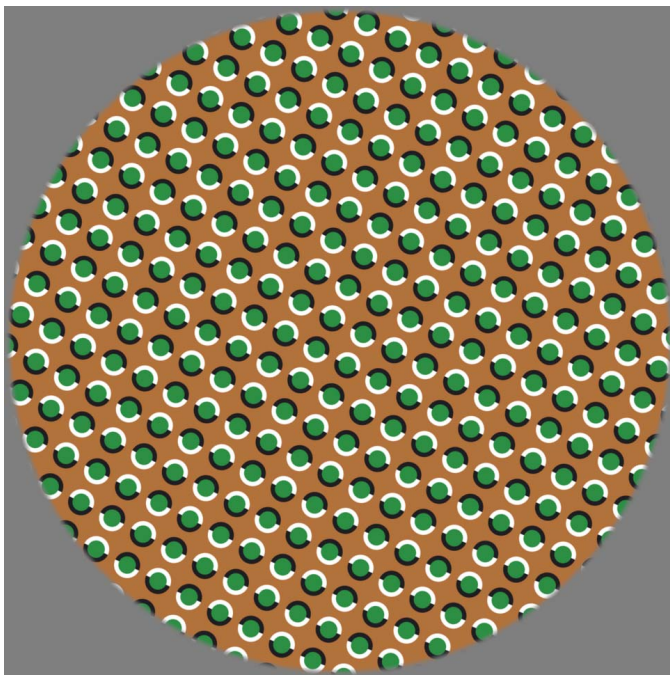


Figure 6. An example of one symmetric pattern (SP) created using the new local hue-adjusted element from Figure 5. Observers report no illusory motion in this pattern.

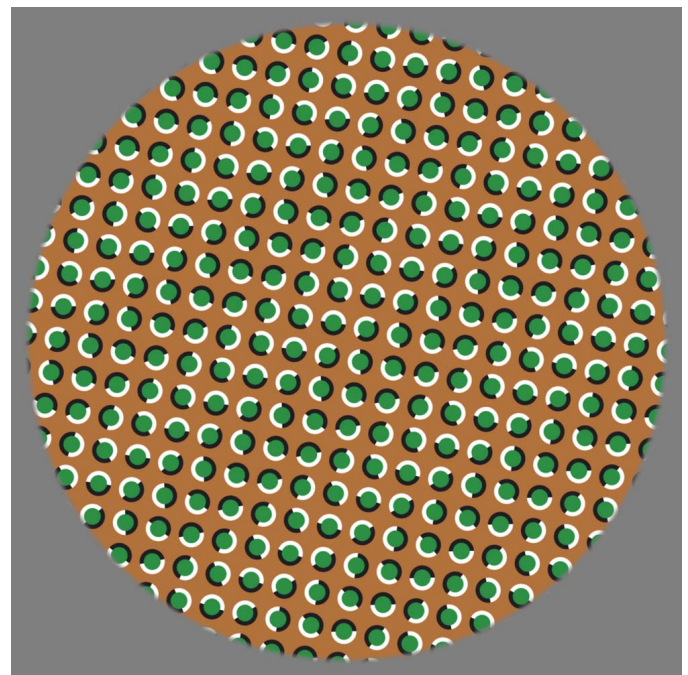


Figure 7. An example of one repeating asymmetric pattern (RAP) created using the new hue-adjusted local element from Figure 5. This pattern contains a less intense peripheral drift illusion.

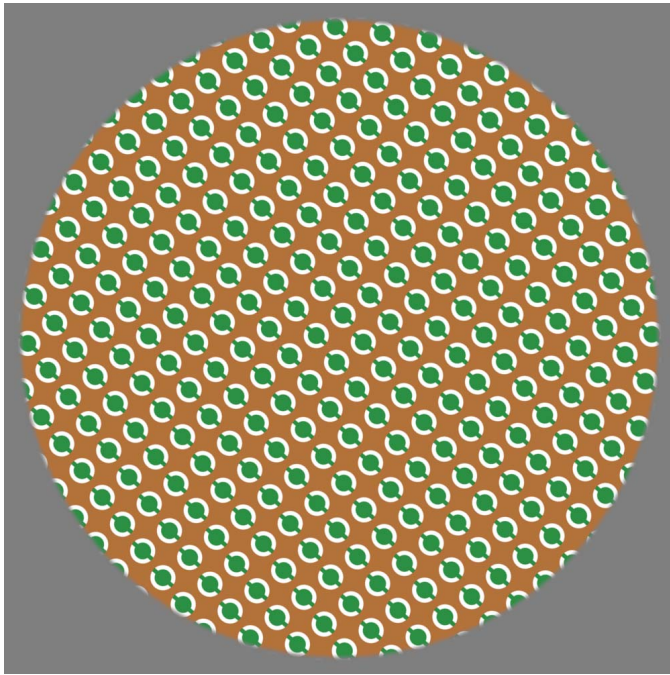


Figure 8. An example of one symmetric pattern (SP) with removal of alternating black/white luminance information. Observers report no illusory motion in this pattern.

Data processing and analysis

Participant data were grouped and all trials were subject to post-experimental processing. Due to the high amount of noise inherent in pupillometry data, and the large amount of data collected at the 60Hz sampling rate (540 samples per trial), samples within trials were excluded from the analysis according to the two following criteria: overly large fixational eye movements and blinks. To remove samples involving overly large fixational eye movements, coordinates outside of a 100-pixel radius from the fixation point for at least 15 samples (0.25 s) were rejected. To remove blink trials, if more than 10 contiguous samples (0.17 s) contained no data, a blink was assumed and the trial was excluded. Finally, if the stimulus phase contained fewer than 100 samples (1.7 s), the whole trial was excluded due to insufficient data. After all exclusions, 78% of the samples remained; all raw data uploaded to the Open Science Framework: <https://osf.io/j2mgf/>.

Data were baseline-corrected to the median pupil-size within the last 200 ms of the preparation phase to normalize the data. Because luminance levels in both conditions images were identical, statistical analyses were focused on the segment of the stimulus phase occurring after pupillary constriction caused by the PLR; analysis of the pupil time-course occurred from minimum pupil size in the stimulus phase (4000 ms) to the start of the blink phase (6000 ms).

We had three sets of predictions. First, within each experiment, we predicted that pupil size would vary by

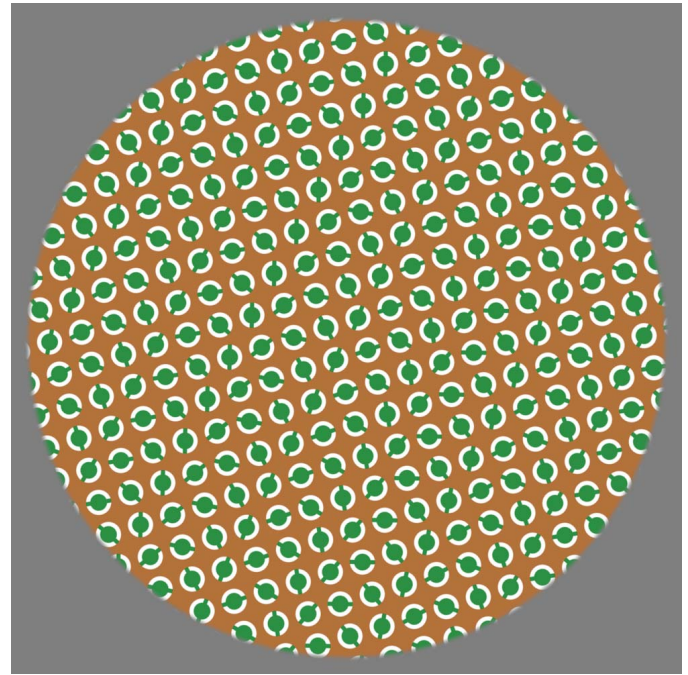


Figure 9. An example of one repeating asymmetric pattern (RAP) with removal of alternating black/white luminance information. This destroyed the perception of illusory motion for the majority of observers, with a very weak perception for a minority.

condition. We used mixed-effect linear regression to predict the pupil size in each trial given the median baseline pupil size and condition, with participant as the random variable. We then used a likelihood ratio test to compare models with and without the condition as a predictor. This test gave a χ^2 statistic which allowed us to see whether the condition predicted pupil size.

Second, we predicted that between-condition pupil size differences would vary across our studies. Here, we used linear regression to predict the average pupil size difference for each block and participant. Using t tests with contrasts, we compared all pupil sizes between all possible pairs of studies. All tests used nondirectional comparisons with a Type I error rate of 0.05 and no family-wise error control. Assumptions were reasonable for all tests. For effect sizes, we use d_R , a robust version of Cohen's d , which shows standardized mean differences (Algina, Keselman, & Penfield, 2005). Square brackets throughout denote 95% bootstrapped confidence intervals.

Finally, to get at the relationship between subjective experience and pupil size, an exploratory Pearson correlation test was conducted comparing the absolute pupil-size difference between RAP and SP patterns and subjective enjoyment ratings for illusory motion in Experiment 1. Data processing and analysis was done using R version 3.3.2 with packages lme4, multicomp, bootES, and ggplot2.

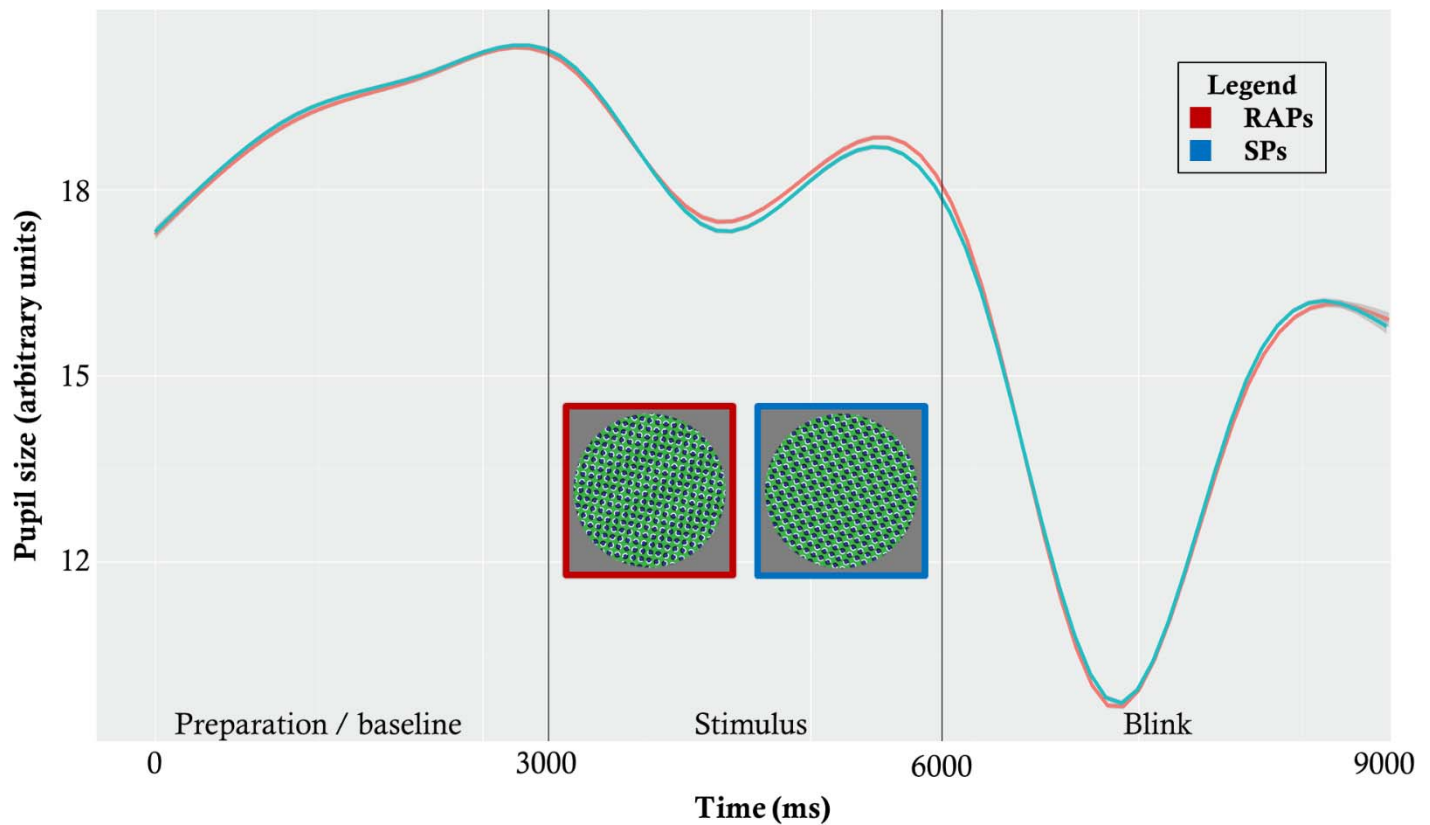


Figure 10. Averaged raw data from Experiment 1. Pupil-size is plotted as a function of time in milliseconds. Vertical lines represent onset and offset of phases outlined in Figure 4: preparation (baseline) fixation from 0–3000 ms, stimulus (RAP vs. SP) fixation phase from 3000–6000 ms, then blink fixation from 6000–9000 ms. Stimulus phase demonstrates existence of effect prior to data processing and analysis decisions. Error bars given by the grey surrounds represent 95% confidence intervals. Lines show LOESS-smoothed curves, as in subsequent plots.

Experiments 2 and 3

Experiments 2 and 3 used the same methods of Experiment 1, with slight stimulus modifications and a new group of participants. The purpose of including these two follow-up experiments was to determine whether any differences in pupillary dilation between the two conditions was due to peripheral drift as predicted, or to the inherent pattern differences necessary to create or destroy the motion illusion in the first place. Possessing the steps for how to create a strong perception of peripheral drift from previous findings, we worked backward to reduce (Experiment 2) and destroy the illusion (Experiment 3) using minimal modifications.

Participants

Thirty-six healthy participants affiliated with McGill University were recruited as observers for this experiment. One participant was excluded due to equipment fault. The remaining 35 participants ranged in age from 18 to 38 years (median = 22; 24 females). Participants

had normal or corrected-to-normal visual acuity and did not possess any abnormalities of the eye.

Stimuli

In Experiment 2, we changed only the hue of the stimuli from Experiment 1. This ensured that everything was kept constant except for the green-blue color pairs. Projecting all possible hues onto a color wheel, we applied a 100° hue subtraction to the entire image produces the new green-orange color pair in the new stimulus set (Figure 5). This effectively reduces the intensity of the perception of peripheral drift, while keeping the distinct black/white patterns in the two conditions the same.

Experiment 3 kept the above stimulus modifications from Experiment 2, but replaced all black regions in the image with white, allowing the center of the local element to extend outward to maintain the necessary orientation information for pattern recognition. This removed the alternating black/white prerequisite for illusory perception, and effectively destroyed the illusion while keeping the distinct patterns in the two

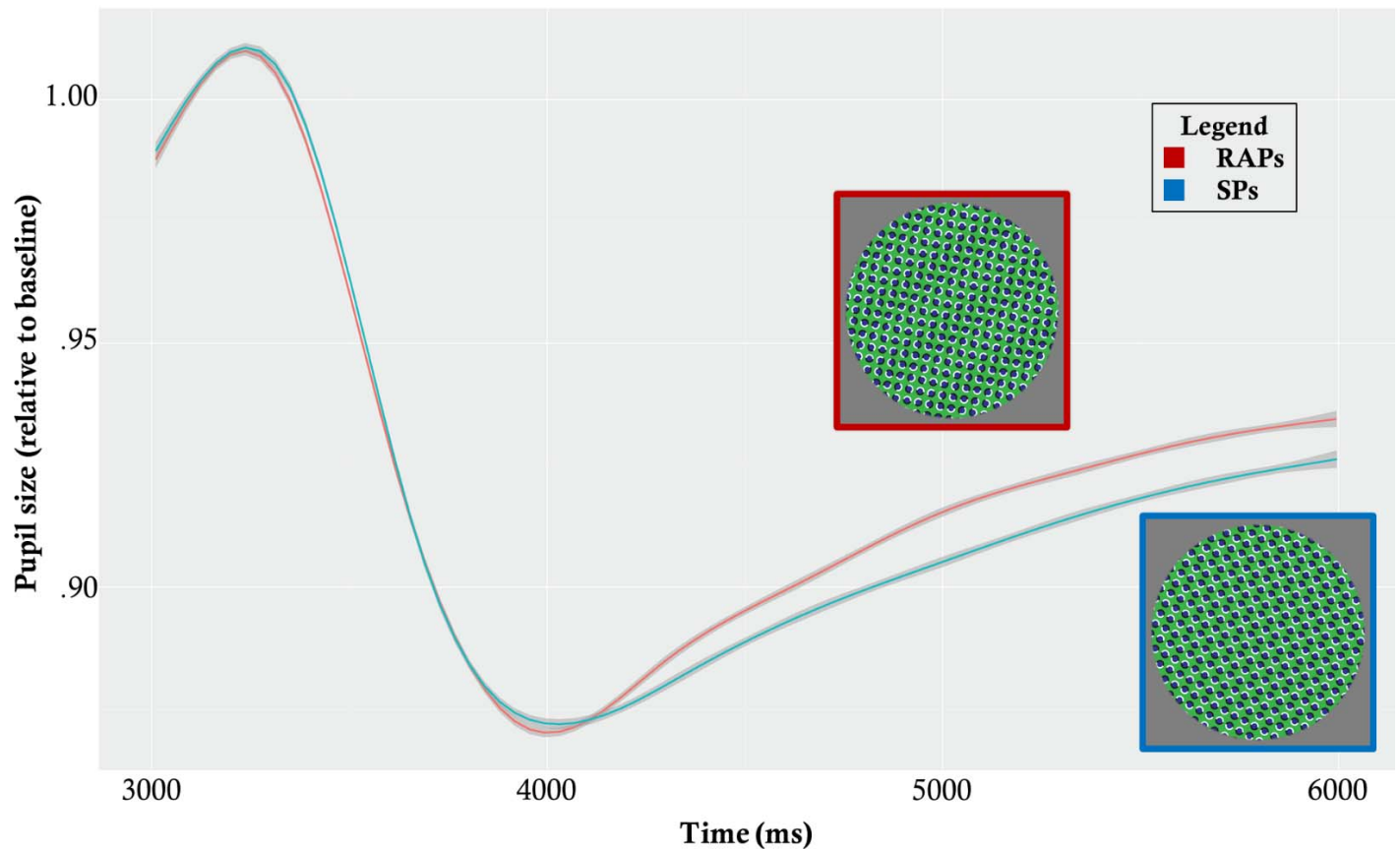


Figure 11. Experiment 1: Strong peripheral drift illusion. Expanded and processed data from the middle portion of Figure 10 (after baseline correction and artefact rejection), revealing the differences between SPs (Figure 2) and RAPs (Figure 3). The illusory motion RAP stimulus (red line) dilates pupils significantly more than the nonillusory SP stimulus (blue line) following the PLR after stimulus onset. Error bars given by the grey surrounds represent 95% confidence intervals.

conditions the same (Figures 8 and 9). The decision to replace black regions with white (rather than white with black) is nested in the finding that, if equal in luminance level, clusters of white in an image do not affect pupil-size differently unless an illusory percep-

tion is occurring (Laeng & Endestad, 2012). Following these two experiments, participants were asked to rate the intensity of the illusory motion on a scale from 1 to 10, using the peripheral drift images of Experiment 1 as a reference.

Results

Pupil sizes were larger when participants viewed the illusions. Thus, pupil dilation for RAPs was significantly greater than SPs for the first two experiments that contained moderate to strong perceptions of the illusory motion [Experiment 1: $\chi^2(1) = 6.536, p = 0.01, d_R = 0.172 (0.031, 0.359)$, Figures 10 and 11; Experiment 2: $\chi^2(1) = 5.73, p < 0.017, d_R = 0.371 (0.103, 0.649)$, Figure 13]. The size of these effects was similar between experiments [$t(283) = -0.225, p = 0.822, d_R = -0.092 (-0.379, 0.224)$]. In Experiment 1, 100% of participants reported observing the peripheral drift illusion (Figure 3). In Experiment 2, 69% of participants reported seeing the illusion with a median

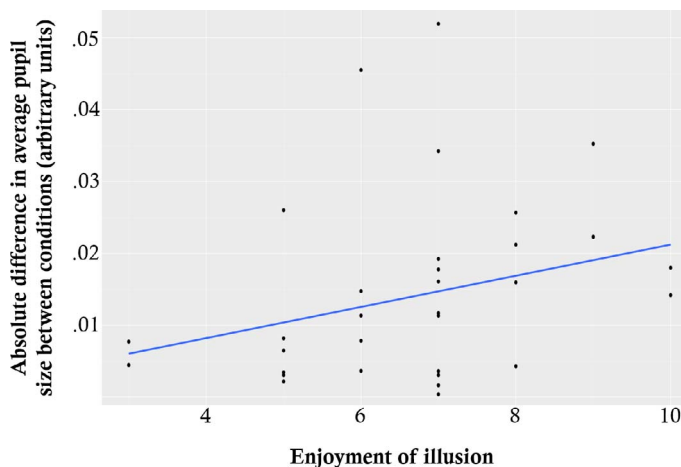


Figure 12. Pupil size differences between conditions correlate with subjective enjoyment of illusory motion.

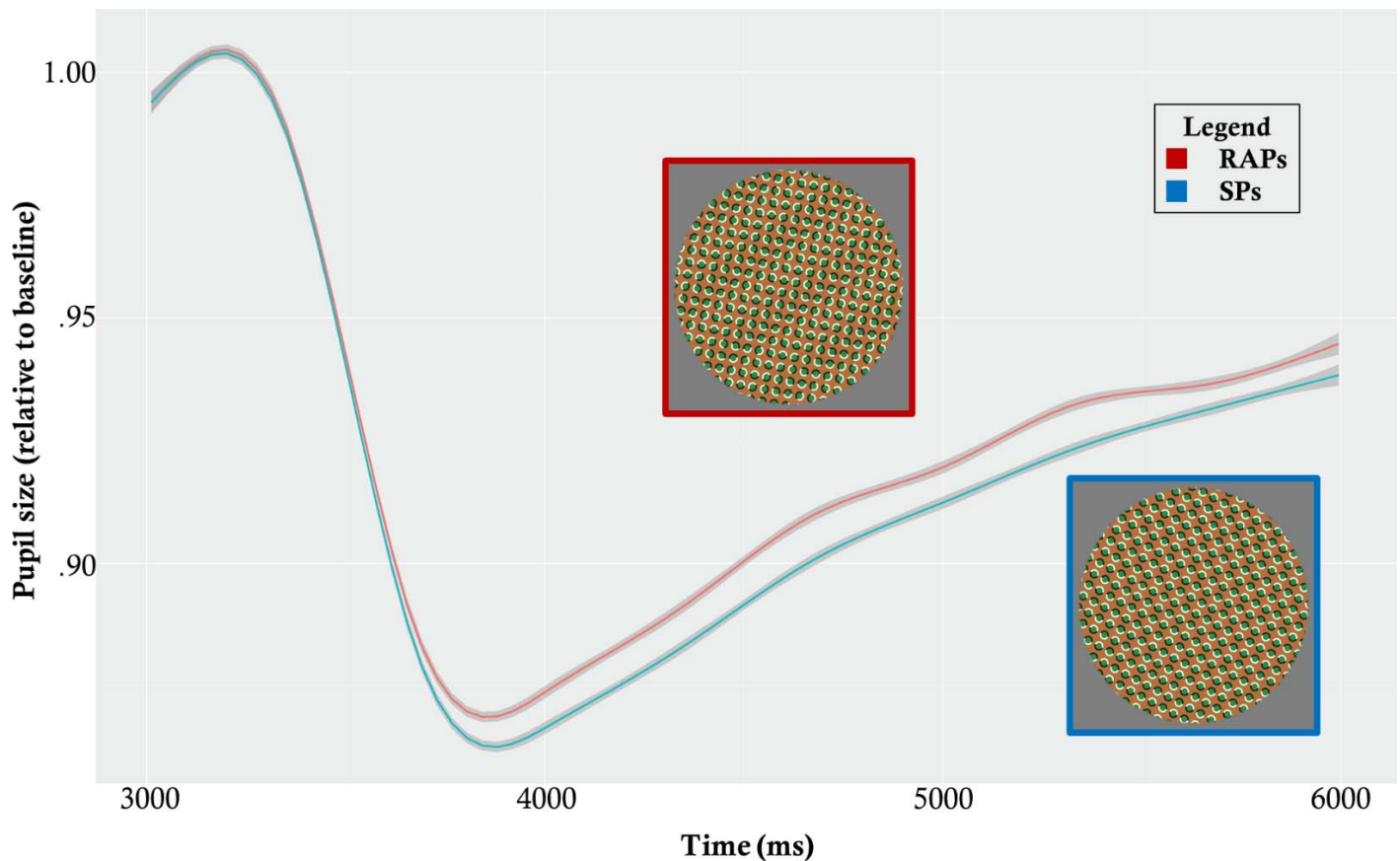


Figure 13. Experiment 2: Moderate peripheral drift illusion. The illusory motion RAP stimulus (Figure 6, red line) dilates pupils significantly more than the nonillusory SP stimulus (Figure 7, blue line) following the PLR after stimulus onset. Error bars given by the grey surrounds represent 95% confidence intervals.

subjective intensity rating of 4 (range: 0–8; Figure 7) when compared with Figure 3. Only in Experiment 1 did every participant perceive the illusory motion, with a statistically significant correlation between absolute difference in average pupil size between SP and RAP conditions and subjective enjoyment ratings for the illusion [Pearson's $r(32) = 0.35$, $p = 0.044$; Figure 12]. Across all experiments, participants reported a median subjective enjoyment rating of 7 out of 10 (range: 1–10) for peripheral drift illusions.

In Experiment 3, pupil size was similar whether or not participants viewed the illusions. Thus, pupil dilation was similar for SP and RAP patterns [$\chi^2(1) = 0.2705$, $p = 0.603$, $d_R = -0.199$ (–0.458, 0.095), Figure 14]. These results differed from Experiments 1 and 2 [Experiment 1: $t(283) = 2.018$, $p = 0.045$, $d_R = 0.419$ (0.077, 0.797); Experiment 2: $t(283) = 2.362$, $p = 0.019$, $d_R = 0.532$ (0.157, 0.910)]. In Experiment 3, only 17% of participants reported seeing the illusion with a median subjective intensity rating of 0 (range: 0–4; Figure 9) when compared with Figure 3. See Figure 15 for a comparison across all studies and conditions.

Discussion

Across three experiments, we investigated the effect of illusory motion on pupil dilation. In our first experiment, we showed that the illusory repeated asymmetric patterns (RAPs) elicited greater pupil dilation than the symmetric patterns (SPs). However, because the observed differences in pupil size could have been the result of inherent pattern differences alone, we conducted a second experiment in which we modified the colors of the RAP images to systematically reduce the intensity of the illusion while preserving their asymmetry. Unexpectedly, even though participants reported the illusion to be weaker than in the first experiment, a similar effect in the pupil data was observed. In a third experiment, we destroyed the illusion in the RAP pattern altogether by removing the alternating black and white regions, and the effect of pupil dilation for RAPs disappeared; the SPs elicited a slightly greater dilation than RAPs. Taken together, these results support the conclusion that illusory motion elicits pupil dilation.

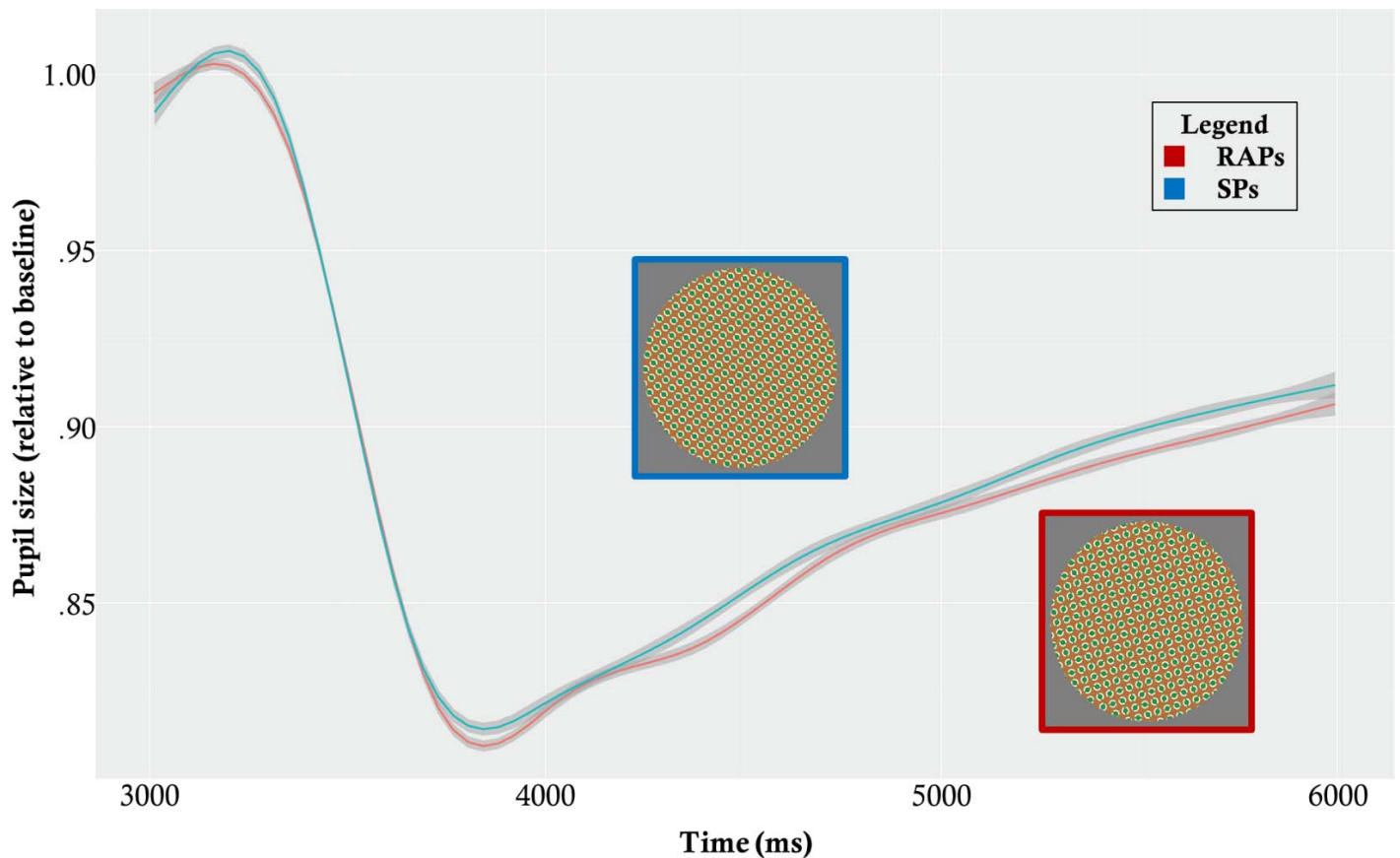


Figure 14. Experiment 3: Weak/absent illusion in RAPs does not dilate pupils more than SPs. Effect shows opposite trend with SPs (Figure 8, blue line) dilating pupils more so than RAPs (Figure 9, red line). Error bars given by the gray surrounds represent 95% confidence intervals.

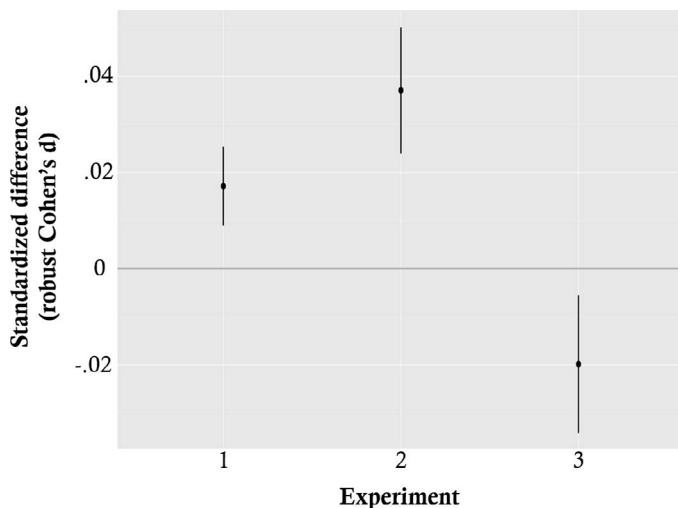


Figure 15. Summary of results. Experiments 1 and 2 showed significantly greater pupil sizes for RAP than SP conditions, whereas Experiment 3 did not. Displayed are the effect-size differences between the three experiments using robust Cohen's d. Experiments 1 and 2 showed significant effect-size differences from Experiment 3, whereas Experiments 1 and 2 themselves did not differ. Error bars show standard error.

Contrary to our initial prediction that the size of the dilation would vary as a function of illusion intensity, similar results were observed for the first two experiments. Despite a marked decrease in proportion of participants able to see the illusion and subjective ratings of intensity for the illusion in Experiment 2, the effect size was not different from Experiment 1. In other words, with our stimuli, the presence of the illusory motion appeared to be more important than its subjective intensity. This could suggest that the pupil response to illusory motion may be an all-or-none mechanism, but this theory would have to be specifically tested with a more well-defined model of illusion strength correlated to participants' subjective ratings. Because the illusion in Experiment 1 was used as a reference for the subjective ratings in Experiments 2 and 3, this analysis was not feasible in the current study.

The greater dilation observed for the RAPs containing the peripheral drift illusion illustrates a potential difference between the underlying perceptual mechanisms for real and illusory motion. For example, in a separate experiment investigating the perception of real motion, the onset of coherent movement generated

in a pattern of dots in random motion triggered systematic constrictions of the pupil that could not be accounted for by the PLR (Sahraie & Barbur, 1997). Given that the onset of real motion has been found to constrict pupils, and our findings demonstrate that the onset of illusory motion dilates pupils, it is possible that separate processes mediate the perception of real vs. illusory motion. One possibility is that illusory motion is inherently arousing, which trumps any effect of real motion on pupil size. Indeed, our positive correlation between illusion enjoyment and pupil size in Experiment 1 supports this theory.

The disappearance of the effect in the last experiment, namely that SPs elicited a slightly greater dilation than RAPs when devoid of any illusory motion, reinforces these conclusions. Perhaps if the patterns themselves were specifically tested, symmetric patterns would dilate pupils more so than asymmetric patterns. Indeed, symmetry has been shown to be more arousing than asymmetry (Bertamini et al., 2013), so in the absence of an illusion it is not surprising that the dilation for RAPs disappeared. A study attempting to demonstrate this should avoid using RAPs though, given that RAPs contain a degree of symmetry as well. For example, in every “repetition” of the asymmetric phase there is mirror symmetry. Additionally, every column in the grid of local elements is translationally symmetric with its neighbors. Therefore, one might expect a greater dilation effect for the SPs if they were compared with a truly asymmetric stimulus. However, the pattern differences in this paper were treated as confounds, and not tested for their physiological relevance.

Peripheral drift is a type of illusory motion that typically requires purposeful eye movements or rapid blinks to activate the illusion (Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008). Here, we show that even with fixation, the sudden onset of peripheral drift images is sufficient to stimulate the perception of illusory motion. This is likely a result of the image onset causing involuntary fixational eye movements, much in the same way that blinking does. Participants reported enjoyment when viewing the peripheral drift images, but their ratings of the perceived intensity of the illusory motion varied considerably. This is not unexpected because a small proportion of individuals (~5%) are incapable of seeing the illusion at all (Chi et al., 2008). This underscores the inherent variability in human vision in perceiving illusory phenomena, and presents an interesting avenue of research given the availability of sensitive methods such as pupillometry for measuring physiological arousal at the single-subject level.

Conclusion

The perception of illusory motion in peripheral drift images elicits a pupillary dilation response. Our findings are counterintuitive to existing evidence showing pupillary constrictions to the perception of motion as well as the associations of arousal made to symmetry. Our results suggest that there are separable mechanisms for the effects on pupil size of illusory versus real motion, and that symmetry is indeed physiologically arousing as asserted in behavioral studies. However, the current investigation does not specifically tackle these issues, and so future studies investigating these phenomena would benefit from a direct comparison between real and illusory motion, and between symmetry and asymmetry on pupil size, at both the group and individual level. One truth remains evident though: visual illusions continue to open doors for scientists to explore the exciting ways that our visual system helps us to understand the world around us, even when those perceptions are fantastic abstractions of reality.

Keywords: visual illusion, illusory motion, peripheral drift, motion processing, pupillometry, pupil dilation, arousal, symmetry

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References

- Algina, J., Keselman, H. J., & Penfield, R. D. (2005). An alternative to Cohen's standardized mean

- difference effect size: A robust parameter and confidence interval in the two independent groups case. *Psychological Methods*, 10(3), 317–328. <http://doi.org/10.1037/1082-989X.10.3.317>
- Backus, B. T., & Oruç, I. (2005). Illusory motion from change over time in the response to contrast and luminance. *Journal of Vision*, 5(11):10, 1055–1069, doi:10.1167/5.11.10. [PubMed] [Article]
- Beatty, J., & Lucero-Wagoner, B. (2000). The pupillary system. *Handbook of Psychophysiology* (2nd ed.). Retrieved from <http://prx.library.gatech.edu/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=psyh&AN=2000-03927-005&site=ehost-live>
- Bertamini, M., Makin, A., & Rampone, G. (2013). Implicit association of symmetry with positive valence, high arousal and simplicity. *I-Perception*, 4(5), 317–327. <http://doi.org/10.1068/i0601jw>
- Binda, P., Pereverzeva, M., & Murray, S. O. (2013). Pupil constrictions to photographs of the sun. *Journal of Vision*, 13(6):8, 1–9, doi:10.1167/13.6.8. [PubMed] [Article]
- Bradley, M. B., Miccoli, L. M., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and automatic activation. *Psychophysiology*, 45(4), 602. <http://doi.org/10.1111/j.1469-8986.2008.00654.x>.The
- Cheetham, M., Wu, L., Pauli, P., & Jancke, L. (2015). Arousal, valence, and the uncanny valley: Psychophysiological and self-report findings. *Frontiers in Psychology*, 6(July), 1–15. <http://doi.org/10.3389/fpsyg.2015.00981>
- Chi, M.-T., Lee, T.-Y., Qu, Y., & Wong, T.-T. (2008). Self-animating images: Illusory motion using repeated asymmetric patterns. *ACM Trans. Graph.*, 27(3), 1–8. <http://doi.org/http://doi.acm.org/10.1145/1360612.1360661>
- Dalmajer, E. S. (2014). Is the low-cost EyeTribe eye tracker any good for research? *PeerJ PrePrints*, 4(606901), 1–35. <http://doi.org/10.7287/peerj.preprints.141v2>
- Dalmajer, E. S., Mathôt, S., & Van der Stigchel, S. (2013). PyGaze: An open-source, cross-platform toolbox for minimal-effort programming of eye-tracking experiments. *Behavior Research Methods*, 46(4), 1–16. <http://doi.org/10.3758/s13428-013-0422-2>
- Ellis, C. J. (1981). The pupillary light reflex in normal subjects. *The British Journal of Ophthalmology*, 65(11), 754–759. <http://doi.org/10.1136/bjo.65.11.754>
- Faubert, J., & Herbert, A. M. (1999). The peripheral drift illusion: A motion illusion in the visual periphery. *Perception*, 28(5), 617–621. <http://doi.org/10.1068/p2825>
- Fraser, A., & Wilcox, K. J. (1979). Perception of illusory movement. *Nature*, 281(5732): 565–566, <http://doi.org/10.1038/281565a0>.
- Hossain, G., & Yeasin, M. (2014). Understanding effects of cognitive load from pupillary responses using Hilbert Analytic Phase. *Computer Vision and Pattern Recognition Workshops (CVPRW), 2014 IEEE Conference*, 375–380. <http://doi.org/10.1109/CVPRW.2014.62>
- Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, 89(1), 221–234. <http://doi.org/10.1016/j.neuron.2015.11.028>
- Kitaoka, A. (2014). Color-dependent motion illusions in stationary images and their phenomenal dimorphism. *Perception*, 43(9), 914–925. <http://doi.org/10.1068/p7706>
- Klingner, J., Tversky, B., & Hanrahan, P. (2011). Effects of visual and verbal presentation on cognitive load in vigilance, memory, and arithmetic tasks. *Psychophysiology*, 48(3), 323–332. <http://doi.org/10.1111/j.1469-8986.2010.01069.x>
- Kloosterman, N. A., Meindertsma, T., van Loon, A. M., Lamme, V. A. F., Bonnef, Y. S., & Donner, T. H. (2015). Pupil size tracks perceptual content and surprise. *European Journal of Neuroscience*, 41(8), 1068–1078. <http://doi.org/10.1111/ejn.12859>
- Laeng, B., & Endestad, T. (2012). Bright illusions reduce the eye's pupil. *Proceedings of the National Academy of Sciences*, 109(6), 2162–2167. <http://doi.org/10.1073/pnas.1118298109>
- Loewenfeld, I. E. (1958). Mechanisms of reflex dilatation of the pupil. *Documenta Ophthalmologica*, 12(1), 185–448. <http://doi.org/10.1007/BF00913471>
- Mathôt, S., van der Linden, L., Jonathan, G., & Vitu, F. (2014). The pupillary light response reflects eye-movement preparation. *Journal of Vision*, 14(10): 203, doi:10.1167/14.10.203. [Abstract]
- Mathot, S., & Van der Stigchel, S. (2015). New light on the mind's eye: The pupillary light response as active vision. *Current Directions in Psychological Science*, 24(5), 374–378. <http://doi.org/10.1177/0963721415593725>
- Naber, M., Frässle, S., & Einhäuser, W. (2011). Perceptual rivalry: Reflexes reveal the gradual nature of visual awareness. *PLoS ONE*, 6(6), e20910. <http://doi.org/10.1371/journal.pone.0020910>
- Palmer, S. E., Schloss, K. B., & Sammartino, J. (2013).

- Visual aesthetics and human preference. *Annual Review of Psychology*, 64(2012), 77–107. <http://doi.org/10.1146/annurev-psych-120710-100504>
- Ripps, H., Chin, N. B., Siegel, I. M., & Breinin, G. M. (1962). The effect of pupil size on accommodation, convergence, and the AC/A ratio. *Investigative Ophthalmology*, 1, 127–135.
- Sahraie, A., & Barbur, J. L. (1997). Pupil response triggered by the onset of coherent motion. *Graefe's Archive for Clinical and Experimental Ophthalmology*, 235(8), 494–500. <http://doi.org/10.1007/BF00947006>
- Stevanov, J., Marković, S., & Kitaoka, A. (2012). Aesthetic valence of visual illusions. *I-Perception*, 3(2), 112–140. <http://doi.org/10.1068/i0455aap>
- Troncoso, X. G., Macknik, S. L., Otero-Millan, J., & Martinez-Conde, S. (2008). Microsaccades drive illusory motion in the Enigma illusion. *Proceedings of the National Academy of Sciences of the United States of America*, 105(41), 16033–16038. <http://doi.org/10.1073/pnas.0709389105>
- Zanker, J. M. (2017). Motion illusions in static patterns. In A. G. Shapiro & D. Todorovic (Eds.), *The Oxford compendium of visual illusions* (Chapter 85, 1–12). Oxford, UK: Oxford University Press.
- Zanker, J. M., Hermens, F., & Walker, R. (2010). Quantifying and modeling the strength of motion illusions perceived in static patterns. *Journal of Vision*, 10(2):13, 1–14, doi:10.1167/10.2.13. [PubMed] [Article]