

# The effect of eye movements and blinks on afterimage appearance and duration

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**The question of whether eye movements influence afterimage perception has been asked since the 18th century, and yet there is surprisingly little consensus on how robust these effects are and why they occur. The number of historical theories aiming to explain the effects are more numerous than clear experimental demonstrations of such effects. We provide a clearer characterization of when eye movements and blinks do or do not affect afterimages with the aim to distinguish between historical theories and integrate them with a modern understanding of perception. We found neither saccades nor pursuit reduced strong afterimage duration, and blinks actually increased afterimage duration when tested in the light. However, for weak afterimages, we found saccades reduced duration, and blinks and pursuit eye movements did not. One interpretation of these results is that saccades diminish afterimage perception because they cause the afterimage to move unlike a real object. Furthermore, because saccades affect weak afterimages but not strong ones, we suggest that their effect is modulated by the ambiguity of the afterimage signal.**

argued that afterimage signals are inherently ambiguous, and this could explain why their visibility is influenced by cues, such as surrounding luminance edges, more than are real stimuli (Powell, Bompas, & Sumner, 2012). Helmholtz (1962) identified another cue that is important to take into account when conducting afterimage experiments:

For obtaining really beautiful positive after-images, the following additional rules should be observed. Both before and after they are developed, any movement of the eye or any sudden movement of the body must be carefully avoided, because under such circumstances they invariably vanish for a while. (p. 231)

Helmholtz's advice is representative of a long tradition of avoiding eye movements during afterimage experiments. Eye movements made during an adaptation phase reduce retinotopic adaptation (Bachy & Zaidi, 2014). The focus of this paper is the effect of eye movements on afterimage perception during the test phase.

## Introduction

Afterimages have always been a founding pillar of vision research from early observations by Greek philosophers (Aristotle, Ross, & Smith, 1910) to the modern day “psychophysicist’s electrode” (Frisby, 1980). They have been explored as interesting phenomena in their own right and are still used to probe countless visual effects. Nonetheless, they are not the easiest tools to work with because they are heterogeneous and perceptually erratic. Previously, we have

## Do saccades suppress afterimage perception?

In addition to Helmholtz (1962), there are several historical observations that saccades cause afterimages to disappear (Darwin & Darwin, 1786; Holt, 1903, as cited in Matin, 1974; Fechner, 1838, as cited in Wade, 1978; Yarbus, 1967), but in-depth empirical studies are few in number. Ferree (1908) published a lengthy analysis of the effect of saccades on weak and strong afterimage fluctuations and durations. One observation

Citation: Powell, G., Sumner, P., & Bompas, A. (2015). The effect of eye movements and blinks on afterimage appearance and duration. *Journal of Vision*, 15(3):20, 1–15, <http://www.journalofvision.org/content/15/3/20>, doi:10.1167/15.3.20.

he reported was that any cue that aided fixation when perceiving an afterimage increased afterimage duration. Further, as fixation was assumed to improve through practice (note that he did not record eye movements), afterimage durations increased. Ferree also used a very small number of participants in his experiments (sometimes only one), and his methods are not reported in such a way that allows full comprehension and replication.

More recently, Fiorentini and Mazzantini (1965) compared the probability of strong, positive afterimages disappearing following saccades, fixation, or tracking (pursuit) eye movements. They reported that 100% of afterimages disappeared following a voluntary saccade with amplitudes above 1° and that a few seconds was required for the afterimage to reappear following the saccade. Unfortunately, these observations were only based on two observers (the authors), and they did not measure afterimage duration or record eye movements.

Kennard, Hartmann, Kraft, and Boshes (1970) measured the duration of suppression immediately following a saccade, using strong afterimages viewed in the dark. They found that suppression time increased with the amplitude of the saccade, and afterimages would completely disappear at saccade frequencies greater than 2 Hz. A positive of this study is that eye movements were recorded; however, the majority of data was drawn from only two observers. The finding that strong afterimages disappear completely during fast saccades is consistent with the perception of one of the authors of the current study, so it remains possible that a significant minority of observers show an effect of saccades.

Finally, Friedman and Marchese (1978) measured the duration of strong positive afterimages generated by flashed targets (viewed in the dark) after one large amplitude saccade (from fixation straight ahead to maximum eccentricity). Unlike previous studies, a large sample size was used (27), and they reported that afterimage duration was reduced by around 50% by the saccade. However, data from only a few participants is actually reported in the paper, and the methods are not detailed enough to allow replication. Furthermore, such large amplitude saccades are not representative of the ones we make most of the time during natural viewing.

Overall, the consensus from the historical literature is that saccades can influence afterimage perception. However, methodological details are often sparse and sample sizes often small, and it may be that the strength of the afterimage matters and/or whether they are viewed in the dark or the light. For example, Yarbus (1967) noted that weak but not strong afterimages were affected, and Hering (1891, as cited in Ferree, 1908) argued specifically that afterimages are not suppressed

in the dark. It has also been claimed that only voluntary eye movements lead to afterimage disappearance because pressing the eyeball to stimulate involuntary movement does not elicit afterimage disappearance (Bell, 1823; Ferree, 1908).

### Why would saccades influence afterimage perception?

Theories to explain the effect of saccades on afterimage perception—if it is real—stretch over two centuries and reflect changes in our understanding of the visual system over the years. However, it is possible to group them into four main categories.

#### *Eyeball and retina*

The first set of theories claim that eye-muscle movement relieves the state of adaptation on the retina. Fechner (1838, as cited in Wade, 1978) argued that eye movements cause vascular and nervous disturbances on the retina, and Flick and Gurber (1889, cited by Exner, 1890; Matin, 1974) suggested that eye movement muscles stimulate the “lymph stream” with new signals, and this enables recovery from adaptation. This set of theories seems the least plausible when evaluated within our modern understanding of the visual system. In particular, we presume the motivation for these theories was based on the false assumption that perceived afterimage duration is determined entirely by the adaptation period of retinal cells, and therefore, that retinal cells must have returned to a nonadapted state for the afterimage to cease being perceived. We now know that cortical mechanisms can greatly influence afterimage intensity and duration, and an afterimage may vanish from conscious perception long before retinal cells recover from adaptation (Powell et al., 2012; van Lier, Vergeer, & Anstis, 2009). This can be simply demonstrated by observing how an afterimage that has already vanished from conscious perception often returns when changing context, for instance, when turning the light off until it vanishes again and then on again and so on. Furthermore, if eye movements enabled a general recovery from adaptation across the retina, this would also affect the ever-present and smoothly changing global adaptation states of the retina (such as von Kries adaptation for color constancy). The specific suppression of small afterimages as perceived objects needs an interpretation in terms of the information and representations supporting perceived objects rather than any direct effect on sensory adaptation. Finally, these theories completely break down if the locus of adaptation sits beyond the retina as has been suggested (McLelland, Baker, Ahmed, & Bair, 2010) although this is still a

contentious topic and recent research suggests that afterimage-generating adaptation is retinal (Zaidi, Ennis, Cao, & Lee, 2012).

### **Visual image changes**

Helmholtz (1962) argued that eye movements produce illumination changes on the retina that lead to afterimage disappearance. This theory seems unlikely given recent work showing that intermittent luminance modulation of the background does not reduce but rather prolongs afterimages (Gerling & Spillmann, 1987; Magnussen & Torjussen, 1974; Matteson, 1965; Robertson & Fry, 1937). Hering (1891, as cited in Ferree, 1908) proposed that retinal image smearing suppresses the afterimage signal, which he claimed to demonstrate by rapidly shifting a piece of paper to mimic smearing. Saccades could also misalign the edges of the afterimage with the background context (e.g., luminance edges), which we know can influence afterimage perception (Daw, 1962; Powell et al., 2012; van Lier et al., 2009). Smearing and misalignment of edges through eye movements are likely causes for why afterimages are not perceived in real life (see Powell et al., 2012, for discussion), but here we test whether they provide sufficient explanation for all afterimage suppression. If so, suppression should not be present when image changes are controlled for by using a homogeneous background. In other words, the present article characterizes whether and why eye movements could cause a reduction in afterimage duration *beyond* the bare consequences they may have on the retinal image.

### **Saccadic suppression**

The third type of theory posits that afterimage perception is diminished by an effect commonly called saccadic suppression but also known as saccadic masking or omission (Campbell & Wurtz, 1978; Ibbotson & Cloherty, 2009; Sylvester, Haynes, & Rees, 2005; Volkmann, 1962). This phenomenon consists of increased thresholds for perceiving real stimuli when presented briefly before, during, or after a saccade. Yarbus (1967) suggested that afterimages disappear during saccades because of the partial inhibition of perception during saccades. Afterimages may be trapped in a continuous state of saccadic suppression during successive fast saccadic eye movements and then return during periods of fixation when the saccade frequency is slower (Kennard et al., 1970). Functional MRI data suggests that saccadic suppression may occur within the lateral geniculate nucleus (LGN) and V1 (Sylvester et al., 2005). Therefore, unlike eyeball and retina theories, saccadic suppression theories assume that afterimage perception is modulated by postretinal areas.

### **Interpretation of ambiguous signals**

Theories in the fourth category focus on higher levels of description and propose that saccades may reduce afterimage perception because they provide evidence against the afterimage signal representing a real object (Exner, 1890; Fiorentini & Mazzantini, 1965). Real objects do not move around with the eyes, and so it is likely that, if an object remains stable on the retina across saccades, it is an artifact of the eye and not an artifact of the world. Coren and Porac (1974) argued that entopic images fade faster during saccades than fixation because the retinal image no longer correlates with the eye-movement signal, and this decorrelation results in a cessation of perceptual responding to the image. This theory shares some similarities with a theory we previously suggested for understanding why afterimages are perceived under some conditions but not others. We suggested that afterimage signals are inherently ambiguous and are thus particularly influenced by cues that increase or decrease the likelihood they represent a real object (Powell et al., 2012). Following this logic, the visual system has learned that real objects do not move with the eyes, and so saccades may suppress afterimages because they decrease the likelihood that the signal represents an object.

### **Could blinks help distinguish theories?**

It follows that, if a clear effect of saccades on afterimage duration can be established in controlled experimental conditions using a homogeneous background, this effect can be accounted mainly in two not necessarily exclusive ways: namely, a fairly low-level process akin to saccadic suppression and a higher-level process related to the disambiguation of visual signals. Although these theories were primarily developed with saccadic eye movements in mind, they also make different predictions regarding blinks. In particular, blinks share many of the oculomotor and suppression mechanisms with saccades (Bodis-Wollner, Bucher, & Seelos, 1999; Bour, Aramideh, & Ongerboer De Visser, 2000; Bour, de Visser, Aramideh, & Speelman, 2002; Bristow, Haynes, Sylvester, Frith, & Rees, 2005; Burr, 2005; Gandhi & Katnani, 2011; Leigh, Newman, Folstein, Lasker, & Jensen, 1983; Ridder & Tomlinson, 1993, 1997; Volkmann, Riggs, Ellicott, & Moore, 1982; Zee et al., 1983), and thus, according to the saccadic suppression theory (category 3), their effect should be expected to be qualitatively similar to saccades. On the other hand, blinks do not cause an afterimage to move unlike a real object and are thus less able than saccades to disambiguate afterimages from real objects. Interpretation of ambiguous signal theories (category 4) predict that afterimage reduction should be greater



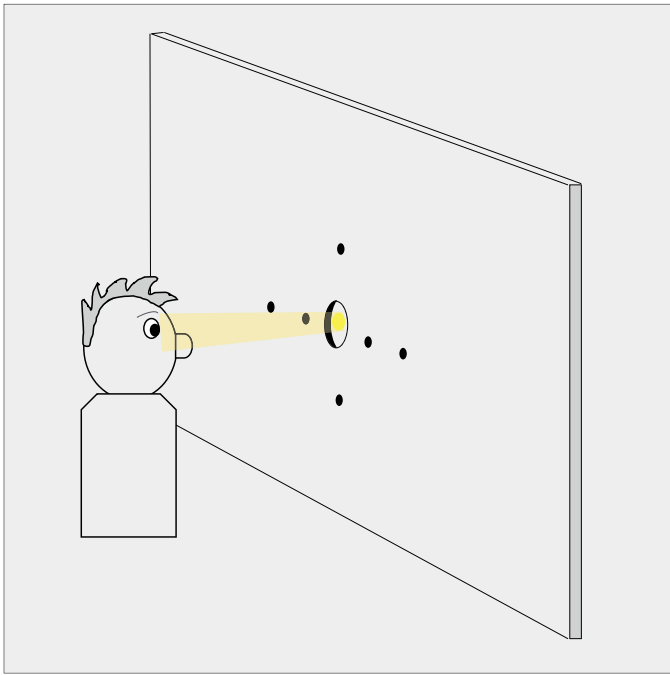


Figure. 1. Apparatus and stimulus display for Experiment 1.

when the afterimages are weaker and thus more ambiguous.

Previous observations on the effect of blinks are inconsistent. Some authors have compared them to saccades and advised that blinking is avoided during afterimage experiments (Helmholtz, 1962; Kennard et al., 1970). Others have suggested that blinks may bring back the afterimage percept once it has faded (Brindley, 1962; Newton, as cited in Wade, 2000; Wang, Munch, Hasler, Prünke, & Larsen, 2008). This is consistent with findings that intermittent luminance changes can increase afterimage duration (Gerling & Spillmann, 1987; Magnussen & Torjussen, 1974; Matteson, 1965; Robertson & Fry, 1937).

### Pursuit eye movements

Both category 3 and 4 theories predict that the effect of pursuit eye movements should not be different from fixation. There is no “pursuit suppression” similar to blink or saccadic suppression, and pursuit eye movements do not cause an afterimage to move unlike a real object. The small amount of research on pursuit eye movements and afterimages suggests that afterimages are perceived to move during pursuit but do not tend to disappear (Darwin & Darwin, 1786; Fiorentini & Mazzantini, 1965). However, the effect of pursuit on afterimage duration is not known. If pursuit afterimages do lead to a reduction in afterimage duration, this would provide evidence against category 3 and 4 theories. On the other hand, previous research has

found evidence of improved visual sensitivity during pursuit (Schutz, Braun, Kerzel, & Gegenfurtner, 2008), so we might expect to find that pursuit eye movements enhance afterimage perception.

### Present experiments

We conducted a detailed exploration of the effects of eye movements on afterimages using historical (Experiment 1) or modern (Experiment 2) apparatus. We measured two common types of afterimages that you might experience in the real world. First, intense afterimages produced by strong adapters; these may be perceived if you were to look at a light bulb or a sunset. Second, weak afterimages generated from less intense light sources; these may be experienced after looking at a colored patch on a computer monitor for a few seconds. Strong, intense afterimages will usually appear positive in the dark (same polarity as the adapting stimulus) and negative in the light (opposite polarity to the adapting stimulus). Although this distinction is not always clear-cut as intense afterimages viewed in the light can appear initially positive before becoming negative. Weak afterimages are usually only seen in the light and will almost always be negative (opposite luminance or color to the adapting stimulus).

In both experiments, we measured afterimage duration during fixation, saccades, blinks, and pursuit. Duration was selected over other measures, such as nulling and matching, because it is easier to equate across eye movement conditions (i.e., a null or match would also have to move with the eyes) and has been used more widely in previous literature.

## Experiment 1: Historical methods

### Observers

Eight naive observers with normal or corrected-to-normal vision participated in Experiment 1 (five males, mean age 28 years). Although naive, all observers had participated in eye movement experiments before, and we know from their previous eye-tracking data that they followed instructions and fixated well.

### Materials and procedure

Chromaticities are reported in CIE color coordinates (chromaticity  $x$ ,  $y$  and luminance  $Y$ ). Apparatus and stimulus display are shown in Figure 1. Observers were seated 42 cm in front of a gray board ( $x = 0.45$ ,  $y = 0.42$ ,  $Y = 14$ ) that was  $140^\circ$  in width and  $100^\circ$  in height. The

adapting stimulus was a 60-W tungsten light bulb ( $x = 0.46$ ,  $y = 0.41$ ,  $Y = 4000$ ) that was viewed through a  $2.5^\circ$  circular aperture. Two inner fixation dots were positioned  $5.5^\circ$  to the left and right of the aperture. Four outer fixation points were positioned  $25.5^\circ$  above, below, to the left, and to the right of the aperture. The fixation points were black in the light condition and phosphorescent in the dark condition ( $x = 0.33$ ,  $y = 0.33$ ,  $Y = 0.1$ ).

At the beginning of each trial, observers were told which condition to expect and given instructions related to this condition. They then fixated either the left or right inner fixation dot, and the adapting stimulus was then presented for 2 s. Directly following this, observers made a saccade to the left outer fixation point if they had adapted at the left inner point or to the right outer fixation point if they had adapted to the right inner point. One of seven eye movement conditions was then presented in one of two environment conditions (in the light or in the dark), totaling 14 main conditions.

In the fixation conditions (conditions 1 and 2), observers remained fixated on the outer point throughout the trial and were asked to minimize blink rate but not to the point of discomfort.

In the fast (3 and 4) and slow (5 and 6) saccade conditions, observers performed saccades around the outer fixation points in response to a tone (1048 Hz) that was played every 450 ms in the fast saccade condition and every 750 ms in the slow saccade condition. Observers were told before the trial whether to saccade clockwise or counterclockwise around the fixation points and were given the opportunity to practice the saccades before the first saccade trial.

In the pursuit conditions (7 and 8), observers followed a laser point that oscillated over an area of  $20^\circ$  at around  $5^\circ/s$  and was controlled by the experimenter from behind the background board.

In the fast (9 and 10) and slow (11 and 12) blink conditions, observers remained fixated on the outer point but were instructed to blink in response to a tone. This tone played every 450 ms in the fast blink condition and every 750 ms in the slow blink condition. In the pursuit plus blink (13 and 14) conditions, observers followed the laser pointer in the same pattern as above while also blinking every 750 ms in response to a tone.

In all conditions, observers reported when the afterimage had disappeared to the experimenter, who marked the time on a stopwatch. This was taken as the measure of afterimage duration. They then described their perception of the afterimage throughout the trial because we were interested in whether the sequence of colors observed for positive afterimages, known as the “flight of colours” (Barry & Bousfield, 1934; Helmholtz, 1962; Wilson & Brocklebank, 1955), was influenced in any way by different eye movement conditions. Yarbus (1967) originally suggested that afterimages would

change color following a saccade, but we are not aware of any research that tests this. Observers were asked specifically about the color and luminance of the afterimage and if this had changed throughout the trial.

As an aside to the 14 main conditions, we were interested in testing the anecdote that blinks can refresh an afterimage once it has faded (Brindley, 1962; Newton, as cited in Wade, 2000; Wang et al., 2008). It is also not known if this effect depends on a luminance change or disruption due to saccadic/blink suppression. To explore this, observers completed two supplementary conditions, both tested in the light or in the dark. These conditions began as a repeat of the fixation condition, but observers were then asked to blink (conditions 15 and 16) or to make a saccade (17 and 18) immediately after the afterimage had faded and report if the afterimage had returned.

Observers completed five trials of each the seven eye movement conditions in both the light and the dark (conditions 1 through 14). They also completed five trials of the two supplementary conditions in both the light and the dark (conditions 15 through 18). Trials in the light and in the dark were run separately over two sessions, and trials of the same condition were completed in blocks. The order of light/dark was counterbalanced across participants, and the order of conditions was pseudorandomized.

## Results

### Afterimage duration during fixation, pursuit, and blinking

Figure 2 shows mean afterimage durations in the 14 main conditions, for light (gray markers) and dark (black markers) environments, during fixation, and six conditions of eye movements.

A  $2 \times 7$  ANOVA was conducted on the afterimage durations with factors of testing environment (light vs. dark) and eye movement conditions (fixation, saccade 450 ms, saccade 750 ms, pursuit, blink 450 ms, blink 750 ms, and pursuit plus blink 450 ms). The assumption of sphericity was violated in the eye movement and eye movement  $\times$  testing environment comparisons, and so these results are reported with the Greenhouse-Geisser correction.

The ANOVA revealed a main effect of testing environment, whereby afterimage duration was longer in the dark than in the light,  $F(1, 48) = 51.9$ ,  $p < 0.01$ . This is to be expected as there is greater potential for adaptation when observers are dark-adapted than light-adapted.

We found a significant eye movement  $\times$  testing environment interaction,  $F(6, 48) = 4.03$ ,  $p < 0.05$ , which

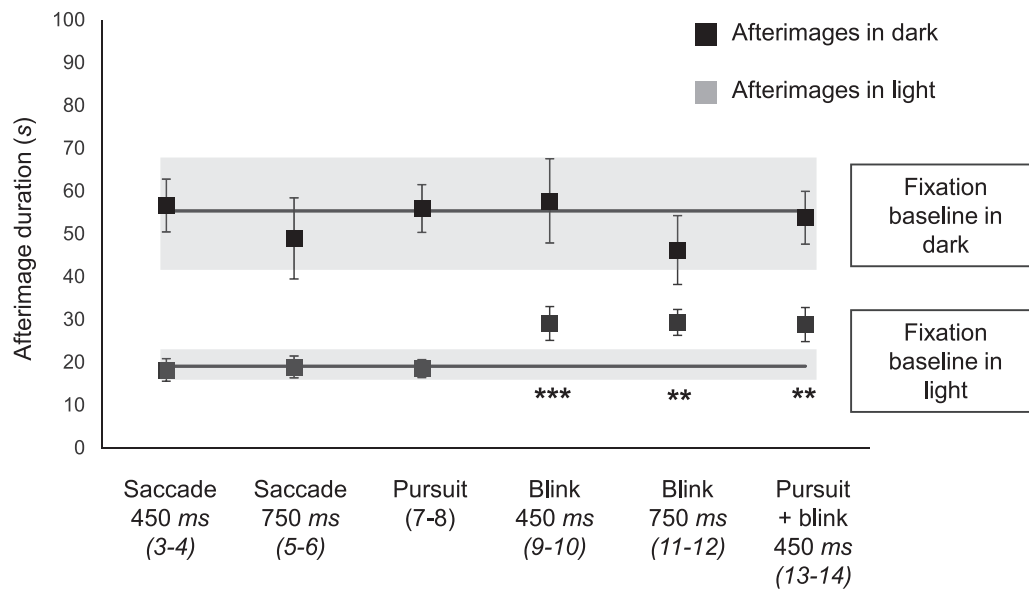


Figure 2. Results from Experiment 1. Mean afterimage durations across observers are shown for the two fixation baseline conditions (1 and 2) and the six other eye movement conditions in dark (black marker) and light (gray marker) environments (conditions 3 to 14). The two lines represent the mean duration of afterimages in the fixation conditions for the dark and the light (gray panels indicate the standard deviation across participants). In the light, afterimages perceived during blinking conditions are consistently longer in duration than the fixation baseline. No difference is found for saccade or pursuit conditions in the light. In the dark, there is no consistent effect of any of the eye movement conditions. Error bars show, for each condition, the 95% confidence intervals of the differences from each participant's mean and thus represent the error that is meaningful to a within-subjects analysis (Loftus & Masson, 1994).

was explored further using simple effects analysis. Afterimages tested in the light were significantly prolonged by blinking every 450 ms ( $p < 0.001$ ) and every 750 ms ( $p < 0.01$ ) relative to the fixation baseline condition. This significant increase in afterimage duration was also found when observers blinked every 450 ms while also pursuing a laser point ( $p < 0.01$ ). These results are consistent with previous findings that luminance changes to the background will prolong afterimage duration (Gerling & Spillmann, 1987; Magnussen & Torjussen, 1974; Matteson, 1965; Robertson & Fry, 1937). This effect is likely due to visual transients produced by the luminance change counteracting perceptual fading of the afterimage. There were no other significant differences in afterimage duration between any of the eye movement conditions.

Although, on average, we did not find an effect of saccades on afterimage duration, a few observers showed the effect in the light. To determine if this was noise or whether the effect was reliable at the individual level, we tested whether each observer's durations in the two saccade conditions were similar. We found a significant correlation between the fast and slow saccade conditions,  $r(6) = 0.76$ ,  $p < 0.05$ , which suggests that within-subject variability was relatively low across similar conditions. Importantly, this correlation was still present when each participant's fixation condition was subtracted from each saccade condition,  $r(6) = 0.75$ ,  $p < 0.05$ , showing that it is

not simply a result of different response bias across participants. This might suggest that the between-subjects differences we observed in the effect of saccades on afterimage duration represent real individual differences rather than noise. This is also reflected in the relatively small error bars for afterimages in the light (see Figure 2). We did not find a correlation between the two saccade conditions in the dark,  $r(6) = 0.38$ , n.s. However, we did find a significant correlation between the slow saccade and slow blink conditions, absolute duration:  $r(6) = 0.79$ ,  $p < 0.05$ ; baseline subtracted:  $r(6) = 0.8$ ,  $p < 0.05$ , and the fast saccade and fast blink conditions, absolute duration:  $r(6) = 0.93$ ,  $p < 0.001$ ; baseline subtracted:  $r(6) = 0.94$ ,  $p < 0.001$ . This perhaps suggests that, in the dark, saccades and blinks of similar frequencies have similar effects on afterimage duration within participants. However, it is certainly the case that variability was higher for afterimages in the dark as demonstrated by much larger error bars (see Figure 2).

### “Refreshing” the afterimage and the “flight of colors”

We explored anecdotal reports that an afterimage will return or “refresh” after it has faded if observers blink and compared this to a condition in which observers made a saccade (conditions 15 through 18).

However, there was no consistent pattern across individuals on these conditions.

The “flight of colors” is a well-known perceptual effect in which, beyond the fact that afterimages in dark environments tend to be positive (brighter than background) and afterimages in light environments tend to be negative (darker than background), an intense positive afterimage cycles through several different (partly idiosyncratic) hues throughout its period of visibility (Barry & Bousfield, 1934; Helmholtz, 1962; Wilson & Brocklebank, 1955). All participants reported this, but we found no suggestion that this systematically changed with eye movements.

## Experiment 2: Modern methods

In Experiment 2, we were interested in the effect of eye movements on weaker afterimages generated from less intense adapters. We updated the methodology so that the stimuli were presented on a CRT screen and eye movements were recorded throughout. The experiment was carried out only in the light because our experience from piloting was that weak afterimages are difficult to perceive in the dark. Observers completed three sub-experiments, which compared fixation baseline trials with five eye movement conditions: slow and fast saccades (Experiment 2a), sinusoidal pursuit (Experiment 2b), and slow and fast blinks (Experiment 2c). Before starting the main experiment, each observer completed a staircase that increased adaptation duration until the duration of their baseline fixation afterimages were longer than 4 s (to prevent floor effects). Thus, the duration of the adapting stimulus was customized to each observer so that afterimage durations were roughly equal across observers. We added an “I did not see an afterimage” response option to our afterimage duration measure, which allowed us to distinguish very short afterimage durations from the time taken to respond when no afterimage was seen at all.

### Observers

Seven naive observers and one author participated in Experiment 2 (four males, mean age 24 years). All had normal color vision and normal or corrected-to-normal visual acuity. Five of the observers also participated in Experiment 1.

### Stimuli and procedure

Stimuli were presented on a 21-in. Sony GDM-F520 Trinitron monitor at 100 Hz, controlled by a Cam-

bridge Research Systems (CRS) ViSaGe and a PC running Matlab. Head movements were limited by a chin rest, and stimuli were viewed binocularly at a distance of 72 cm. Manual responses were made with a CRS CB6 button box. Observers were tested with the lights off.

Example trials are shown in Figure 3. The adapting stimuli were green ( $x = 0.25$ ,  $y = 0.49$ ,  $Y = 29$ ) or pink ( $x = 0.30$ ,  $y = 0.17$ ,  $Y = 29$ )  $3^\circ$ -diameter circles, presented  $4^\circ$  to the right/left of center. Observers fixated a black  $0.15^\circ$  dot in the center of the adapting stimulus. The adapting stimulus was removed after the adaptation duration that was set for each observer in the pilot study, leaving the dot used to direct the eye movements. For Experiment 2a (saccades vs. fixation), the dot continuously jumped from left to right of the screen every 600 ms (1.67 Hz) or every 300 ms (3.34 Hz). In Experiment 2b (blinks vs. fixation), the fixation dot always remained in the center of the screen, and observers were instructed to blink in response to a 0.1-s low-frequency tone. In the slow blink condition, the tone was played every 600 ms (1.67 Hz blink frequency), and in the fast blink condition, the tone was played every 300 ms (3.34 Hz blink frequency). Observers were instructed to avoid blinking unless a tone was played. In Experiment 2c (pursuit vs. fixation), the dot smoothly and continuously translated (in a sinusoidal pattern) from left to right at a rate of 0.33 Hz with a maximum eccentricity of  $4^\circ$  on either side. During fixation baseline trials in Experiments 2a through c, the dot remained stationary (same location as adaptation), and no tone played.

Observers were instructed to remain carefully fixated on the dot at all times even when it moved. Observers pressed a response box key when they perceived that the afterimage had completely faded and a different key if they did not see an afterimage at all on that trial. All trials were terminated once a response was collected. To reduce carryover adaptation, the trials ended with a 600-ms animated mask consisting of multiple  $3^\circ$  circles randomly changing position and chromaticity at 100 Hz. Observers received 32 repetitions of each eye movement condition. Before starting the experiment, observers first completed a short pilot in which adaptation duration was increased until four consecutive afterimage durations during fixation were above 4 s. One observer failed to reach the criterion of 4 s and so was tested with an adaptation duration of 6 s.

### Eye movement analysis

Eye movement traces were recorded with a CRS high-speed video eye tracker sampling at 250 Hz and smoothed with a Gaussian filter ( $SD = 4$  Hz). The samples during the afterimage measurement phases



## Fixation baseline (Expt 2a-c)

## Saccade (Expt 2a)

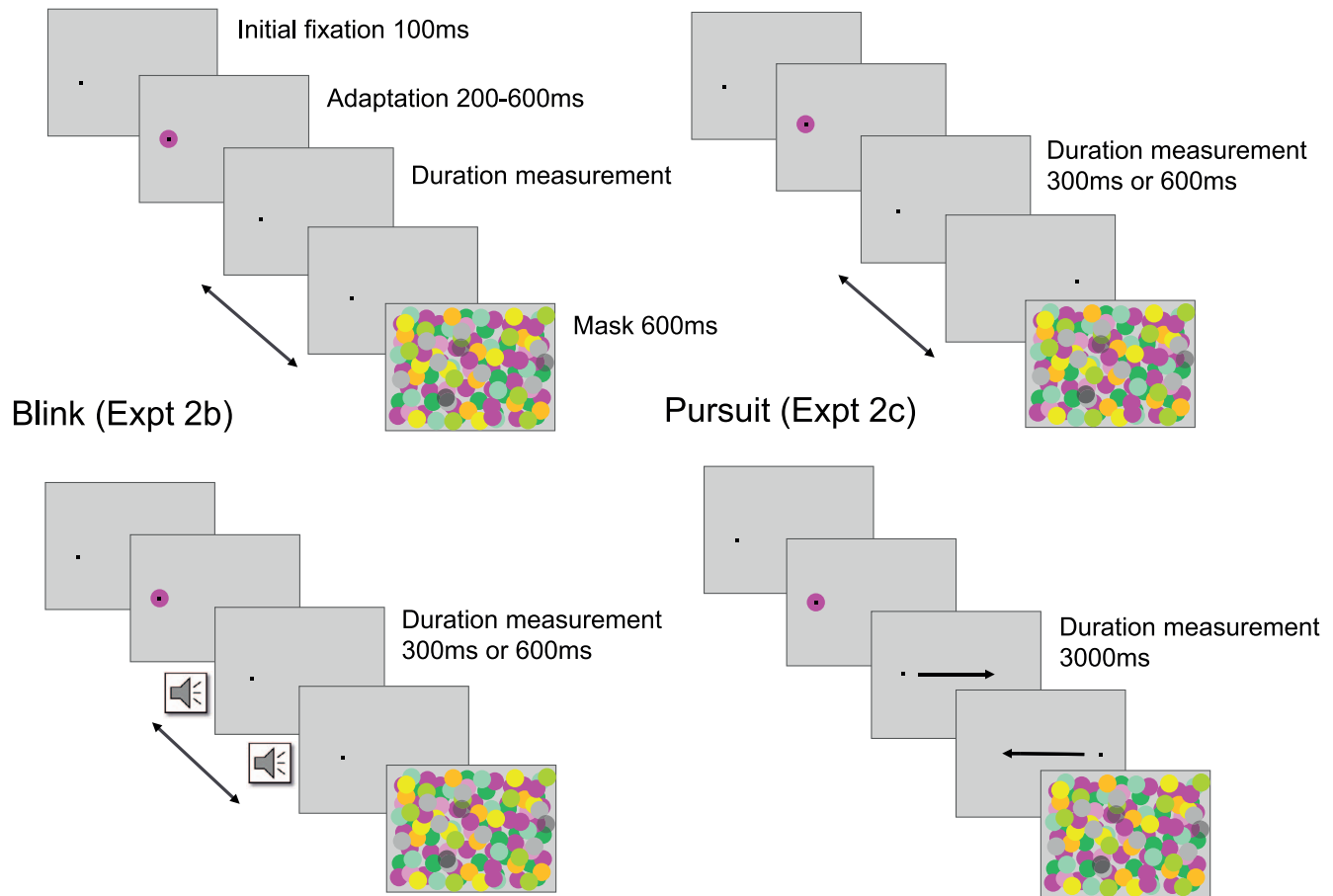


Figure 3. Example trials from Experiment 2. Fixation baseline (Experiment 2a through c): Observers adapted to a green/pink patch presented on the left or the right. The adaption patch was then removed, leaving a fixation dot. Observers then indicated when the afterimage had faded. Trials ended with a mask to reduce carryover adaptation. Saccades (Experiment 2a): Trial is identical to fixation baseline, but fixation dot jumps from side to side every 300 ms (fast saccade) or 600 ms (slow saccade) during afterimage measurement phase. Blinks (Experiment 2b): identical to fixation baseline, but observers blink in time with a metronome every 300 ms (fast blink) or 600 ms (slow blink). Pursuit (Experiment 2c): as above, but fixation dot smoothly translates from side to side every 3000 ms.

were analyzed to distinguish blinks from saccadic eye movements. Saccades were detected if their jerk (derivative of the eye acceleration, see Wyatt, 1998) exceeded a criterion of  $30^\circ/s^3$ . Fixation and pursuit trials that contained saccades or blinks were discarded to reduce cross-condition contamination (this resulted in the exclusion of less than 5% of the trials).

## Results

Comparisons between the eye movement subexperiments (saccade: Experiment 2a, blink: Experiment 2b, and pursuit: Experiment 2c) and their respective fixation baseline conditions were conducted separately

because they were run over distinct sessions. As shown in Figure 4A, saccades reduced afterimage duration relative to fixation [ANOVA main effect:  $F(2, 12) = 11.44$ ,  $p < 0.01$ ; comparisons between fixation and 1.67- and 3.34-Hz saccade frequency, both  $ps < 0.05$ ]. This effect increased with the frequency of the saccades; afterimage durations during 1.67-Hz saccades were significantly longer than during 3.34-Hz saccades ( $p < 0.05$ ). The difference between fixation and saccades is also reflected in the finding that observers were more likely to see the afterimage at all during fixation than saccades (Figure 4B), ANOVA main effect:  $F(2, 12) = 4.29$ ,  $p < 0.05$ , comparisons between fixation and slow and fast saccade, both  $ps < 0.05$ ). There were no other significant differences between the eye movement conditions and their fixation baselines. The average



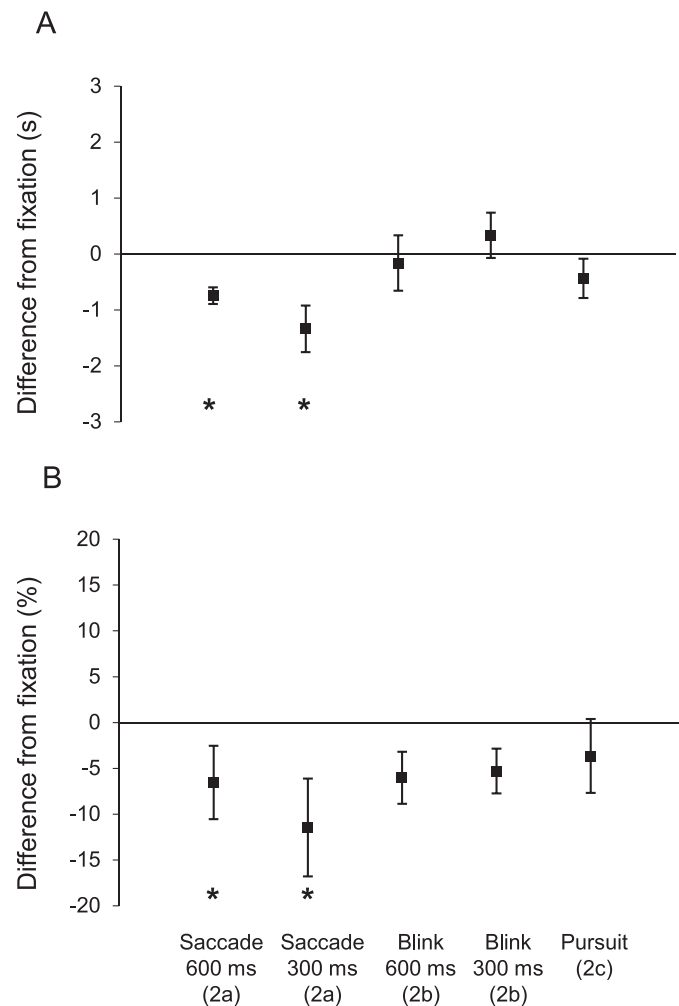


Figure 4. Results from Experiment 2a through c. (A) Duration. Mean difference in afterimage duration from baseline fixation condition for slow saccade (Experiment 2a), fast saccade (Experiment 2a), slow blink (Experiment 2b), fast blink (Experiment 2b), and pursuit (Experiment 2c). Afterimage duration decreases during saccades relative to fixation, and duration for 3.34-Hz saccades is shorter than for 1.67-Hz saccades. Durations during pursuit and blinks are not significantly different from fixation baseline. (B) Percentage of trials in which afterimage was seen. Mean difference in the percentage of trials in which afterimage was seen compared to fixation baseline. Percentage of trials in which an afterimage was seen is higher during fixation than either fast or slow saccades. The percentage of trials in which an afterimage was seen is not reduced during pursuit and blinks relative to fixation. Error bars show the 95% confidence intervals of the differences from each participant's mean (Loftus & Masson, 1994). Error bars are sometimes smaller than the marker size.

baseline fixation durations for each session were all above 4 s; thus the results cannot be attributed to floor effects (mean baseline in saccade session = 4.41 s, blink session = 4 s, pursuit session = 4.5 s).

## Discussion

Using first historical and then modern apparatus, we explored the effect of saccades, pursuit, and blinks on afterimage duration. Our aim was to test previous reports that saccades reduce afterimage perception, to differentiate a number of suggested theories for this

effect, and to frame them within our modern understanding of vision science.

### When do eye movements influence afterimage perception?

We found that saccades reduce the duration of weak but not strong afterimages. The effect for weak afterimages increased with the frequency of the saccades. Saccades also significantly decreased the likelihood that weak afterimages were seen at all although this effect did not significantly increase with saccade frequency. Blinks and pursuit eye movements

	Eyeball and retina	Visual image changes	Saccadic suppression	Interpretation of ambiguous signals
AI viewed on homogenous backgrounds affected by saccades	✓	✗	✓	✓
Disappearance longer for AIs than real stimuli	✓	✓	✗	✓
AIs disappear after saccade then return	✗	✓	✓	✓
Global adaptation states are not affected by saccades	✗	✓	✗	✓
Other ocular muscle contractions (e.g., blinks) do not affect AIs	✗	✓	✗	✓
Consistent with current understanding of visual system	✗	✓	✓	✓
During very fast saccades, AIs do not return	✗	-	✓	✓
Pursuit eye movements do not reduce AI perception	✗	-	✓	✓
Perception of weak AIs suppressed more than strong AIs	✗	-	✗	✓
Underlying neural mechanism is relatively well established	✗	✓	✓	✗

Table 1. What we know about the effect of eye movements and blinks on afterimages (AIs) compared against the four theories for the effect of saccades. *Notes:* If a theory can explain or is compatible with a particular effect, it is marked ✓; if it cannot explain or is not compatible with an effect, it is marked ✗; and if we cannot tell either way, it is marked -. Please note that this table relies on a binary classification system that may be oversimplified and is only meant to be a guide to support the main discussion.

did not decrease the duration of low- or high-intensity afterimages relative to fixation. In fact, blinks increased strong afterimage duration in the light.

Our results are not consistent with previous reports that saccades reduce the duration of strong afterimages (Ferree, 1908; Friedman & Marchese, 1978; Kennard et al., 1970). This discrepancy cannot be attributed to differences in the amplitude and frequency of the saccades as these were similar to past reports. It is possible that differences in design could explain our divergent findings although it is often difficult to draw direct comparisons between our study and historical findings due to the sometimes opaque description of methodology. In particular, the adapting stimuli we used were slightly less intense than some previous work (e.g., Friedman & Marchese, 1978; Kennard et al., 1970) although still sufficient to generate a strong, long-lasting afterimage. Another possibility is that observers did not comply with the instructions to saccade, and we cannot test this explicitly because we did not record eye movements in Experiment 1. Further, observers' head movements were not constrained by a chin rest, which could have resulted in some additional movement. However, our observers were all experienced in psychophysics experiments and had performed eye movements and fixated reliably on cue in the past. We also found a strong effect of blinking on afterimage duration, and there is no reason to expect that observers would comply with the instruction to blink but not to saccade.

Our sample size of eight observers is considerably higher than most other studies, in which two to three is average. It is possible that the saccade effect on afterimages is more open to large between- and within-subjects variability than many of the robust effects found in perception studies. The between-participants differences we observed in the light may reflect genuine

individual differences, rather than just measurement or perceptual noise, given that the results were strongly correlated across saccade conditions. Such individual differences, if genuine, may be in keeping with individual differences in reversal/visibility durations for other ambiguous phenomena, such as binocular rivalry and multistable figures (Aafjes, Hueting, & Visser, 1966; Frederiksen & Guilford, 1934; Kanai, Bahrami, & Rees, 2010; Kleinschmidt, Sterzer, & Rees, 2012). In the dark, within- and between-subjects variability was very large. Although we did find that similar frequency blink and saccade conditions correlated with each other, suggesting some reliability within participants. A final point to ponder is whether our results have uncovered a classic filing drawer problem, where it has rarely been noted when saccades did not reduce afterimage duration.

### Why do saccades and blinks influence afterimage perception?

In the Introduction, we discussed four possible theories for why saccades affect afterimage perception. Table 1 shows a summary of whether each snippet of available evidence is consistent with each theory. This table is meant as a summary to help the reader separate the four theories rather than an exhaustive reproduction of past findings.

Afterimages generated by strong stimuli are likely due to photochemical bleaching (Williams & Macleod, 1979). Possible origins within the LGN or at the cortical level have been proposed for afterimages generated by weak stimuli (e.g., McLelland, Ahmed, & Bair, 2009; McLelland et al., 2010; Shevell, St Clair, & Hong, 2008; Shimojo, Kamitani, & Nishida, 2001) although the most recent work argues strongly that

these afterimages most likely originate at the retinal ganglion cell level (Zaidi et al., 2012). In any case, it is clear that our perception of them is modulated by cortical mechanisms (Bachmann & Murd, 2010; Feldman, Todman, & Bender, 1974; Hazenberg & van Lier, 2013; Powell et al., 2012; van Boxtel, Tsuchiya, & Koch, 2010). They will often fade from consciousness before the adaptation has recovered unless they are bolstered back to awareness by a surrounding luminance edge or a sudden change in background luminance (Matteson, 1965; Powell et al., 2012; van Lier et al., 2009). Further, changes in the perceived size of afterimages when they are viewed on backgrounds of varying distances have been correlated with blood oxygen level-dependent responses in V1 (Sperandio, Chouinard, & Goodale, 2012), providing further evidence that our perception of afterimages is influenced by cortical processes. Thus a purely retinal locus (theory category 1) is unlikely for eye movement effects. Moreover, blinks and, indeed, fixation and pursuit all produce contractions of the ocular muscles (Evinger, Shaw, Peck, Manning, & Baker, 1984; Leigh & Zee, 1999; Scott & Collins, 1973) and yet do not reduce afterimage duration.

That blinks do not reduce perceived afterimage duration also casts doubt on saccadic suppression theories (category 3) because blink suppression is similar in time course and magnitude to saccadic suppression (Burr, 2005; Ridder & Tomlinson, 1993, 1997; Volkmann et al., 1982). Saccadic suppression and blink suppression have also been linked to similar cortical areas by fMRI research (Bristow et al., 2005; Sylvester et al., 2005). It is also possible that the effect of blinks is a mixture of reduction (due to suppression as with saccades) and enhancement (due to luminance background changes). These opposing effects may have nulled each other in Experiment 2, leading to no reduction or increase in afterimage duration during blinks relative to fixation. This explanation relies on two untested assumptions: that intermittent luminance backgrounds can prolong weak afterimages as well as intense afterimages and that the enhancement effect of blinks does not rely on seeing the positive afterimage during the dark phase (which does not happen for weak afterimages). The suppression and enhancement effects would also need to be roughly equal in strength (within the range of measurement noise) in order to result in a null. A more general counterargument to category 3 theories is that saccadic suppression only lasts for 50–100 ms, and so the saccade frequency would need to be extremely high to cause an afterimage to disappear completely. It is also unclear whether saccadic suppression should be expected to be stronger for weak rather than strong signals. Altogether, although it is possible that saccadic suppression participates in the observed reduction of weak afterimage duration by

saccadic eye movements, it seems unlikely that it is the sole explanation for it.

Changes to the visual image (category 2) are likely to influence afterimage perception, in particular changes to background edges that often accompany saccades (Daw, 1962; Powell et al., 2012). However, we controlled for these by testing on homogenous backgrounds and still found an effect of saccades on weak afterimages, which suggests that context cannot wholly account for this effect.

Taken together, our results are consistent with theories (category 4) that saccades reduce afterimage duration because they cue the visual system that the afterimage is not a real object (Coren & Porac, 1974; Exner, 1890; Fiorentini & Mazzantini, 1965). Previously, we have suggested that afterimage signals are inherently ambiguous, and this produces a degree of perceptual uncertainty over whether to perceive them (Powell et al., 2012). This uncertainty then leads them to be particularly influenced by cues that increase or decrease the likelihood that they represent a real object. In support of this theory, we found that afterimages benefit more from contextual edge cues than real stimuli of similar appearance. On the other hand, saccadic eye movements may decrease the likelihood that the afterimage represents a real object, leading to a reduction in afterimage duration and a decrease in the probability that the afterimage is perceived at all.

This theory can explain why afterimage suppression would occur when eye movements misalign them with visual image cues (category 3) but can also occur when viewed on homogenous backgrounds because the movement itself is a cue. It also predicts that blinks and pursuit eye movements would not reduce afterimage duration as we found. Under this theory, the explanation for afterimage suppression would be extended to any other image stabilized on the retina, such as those arising from materials in the eye (entopic images); these also disappear more quickly during saccadic eye movements (Coren & Porac, 1974; Exner, 1890). It also offers two explanations for why weak afterimages in Experiment 2 were suppressed and strong afterimages in Experiment 1 were not. First, weak afterimages may be suppressed more by saccades because their signals are more ambiguous. Second, the background screen was smaller in Experiment 2 than in Experiment 1, and so there were more peripheral changes across saccades in Experiment 2, which could have provided more reference cues that the afterimage was moving unlike other objects in the scene. Future work could explore in more detail the relationship between saccades and background context changes.

One criticism of category 4 theories is that they do not point to an underlying mechanism. However, other events occur around the time of a saccade, but it is unclear whether these could offer complementary or

alternative explanations or whether they can account for the differential effect of saccades on strong and weak afterimages. One explanation relates to trans-saccadic integration and remapping, with which attention is shifted to a postsaccadic location before a saccade by remapping of receptive fields (Melcher, 2007, 2009; Melcher & Colby, 2008; Merriam, Genova, & Colby, 2007; Nakamura & Colby, 2002). This remapping allows receptive fields at postsaccadic locations to shrink and shift toward the saccade target to improve visual sensitivity (Tolias et al., 2001). These processes may explain findings that the perceived hue of a stimulus presented in a future fixation position biases the perceived hue of a stimulus presented postsaccadically at the same spatial but different retinal location (Wittenberg, Bremmer, & Wachtler, 2008). When the predicted hue of a postsaccadic location differs widely from the perceived hue after the saccade (due to the presence of an afterimage), the brain may attempt to compensate for the discrepancy to maintain perceptual stability. Thus, in our experiments, the visual system has knowledge that the postsaccadic location is not the same hue as the afterimage, which could produce bias in afterimage perception toward the background. As our backgrounds were gray, this would translate to a decrease in afterimage saturation following a saccade.

More generally, it has been proposed that associations are formed between eye movement signals and responses of visual neurons through experience (Bompas & O'Regan, 2006; Bompas, Powell, & Sumner, 2013). These associations may underlie how the visual system learns to anticipate the visual response to objects in the world as the eyes move around it. This not only enables the world to remain stable on the retina, but also allows the visual system to distinguish what is in the world from what is only on the retina. A possible learned assumption is that the world remains stable most of the time. Therefore, if a patch on the visual field changes hue across a saccade (e.g., when it is viewed first in the periphery and then in the fovea), it is likely that this hue change is due to artifact of the retina and not an object in the world. This is exactly the situation produced by afterimages and other stabilized images across saccadic eye movements.

These mechanisms might result in greater consequences for the perception of weak afterimages than strong afterimages, in that the former may be completely extinguished by eye movements and the later are merely diluted. This pattern is not obviously predicted by trans-saccadic integration models and may rather suggest the presence of higher levels of interpretation that weigh up the ambiguity of the afterimage signal. A more specific description of these mechanisms requires much further study, however.

## Why do blinks influence afterimage duration?

One explanation for why blinks increased the duration of strong afterimages in the light is that they provide a luminance transient that counteracts perceptual fading mechanisms in the cortex (Brindley, 1962). Adaptation signals are stabilized on the retina and are conveyed to the cortex as a steady signal, where their representation fades before the retina recovers from adaptation. A visual transient accompanied by the still-existing afterimage signal from the retina may be sufficient to reinvigorate a neural representation of this signal. This could explain why blinks and other types of intermittent luminance background prolong afterimage duration (Gerling & Spillmann, 1987; Magnussen & Torjussen, 1974; Matteson, 1965; Robertson & Fry, 1937).

## Summary

Our research here suggests that saccadic eye movements are more likely to reduce the perception of weak afterimages than intense afterimages. Blinking seems to increase the duration of intense afterimages in the light but has no effect on weak afterimages. Pursuit eye movements do not seem to affect the perception of weak or intense afterimages. We argued that these findings are most consistent with the idea that saccades reduce afterimage perception because they support the interpretation that the afterimage is not a real object. We also found that, particularly for intense afterimages viewed in the light, some observers showed an effect of saccades and others did not. These individual differences may be genuine as there was a good correlation within observers between the two saccade conditions. Just to be safe, however, it is probably still best to follow Helmholtz's (1962) advice and avoid eye movements when conducting afterimage experiments.

*Keywords:* afterimages, saccades, pursuit, blinks

## Acknowledgments

This work was supported by a PhD studentship from the BBSRC and Cardiff University, and a grant from the ESRC (ES/K002325/1). Thank you to Tom Freeman for help and advice with eye movement and blink analysis.

Commercial relationships: none.

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## References

- Aafjes, M., Hueting, J. E., & Visser, P. (1966). Individual and interindividual differences in binocular retinal rivalry in man. *Psychophysiology*, *3*(1), 18–22.
- Aristotle, Ross, W. D., & Smith, J. A. (1910). *The works of Aristotle* (Vol. 3). Oxford, UK: Clarendon Press.
- Bachmann, T., & Murd, C. (2010). Covert spatial attention in search for the location of a color-afterimage patch speeds up its decay from awareness: Introducing a method useful for the study of neural correlates of visual awareness. *Vision Research*, *50*(11), 1048–1053, doi:10.1016/j.visres.2010.03.013.
- Bachy, R., & Zaidi, Q. (2014). Factors governing the speed of color adaptation in foveal versus peripheral vision. *Journal of the Optical Society of America*, *31*(4), A220–A225.
- Barry, H., Jr., & Bousfield, W. (1934). Implications of the flight of colors. *Psychological Review*, *41*(3), 300.
- Bell, C. (1823). On the motions of the eye, in illustration of the uses of the muscles and nerves of the orbit. *Philosophical Transactions of the Royal Society of London*, *113*, 166–186.
- Bodis-Wollner, I., Bucher, S. F., & Seelos, K. C. (1999). Cortical activation patterns during voluntary blinks and voluntary saccades. *Neurology*, *53*(8), 1800–1805.
- Bompas, A., & O'Regan, J. K. (2006). Evidence for a role of action in colour perception. *Perception*, *35*(1), 65–78.
- Bompas, A., Powell, G., & Sumner, P. (2013). Systematic biases in adult color perception persist despite lifelong information sufficient to calibrate them. *Journal of Vision*, *13*(1):19, 1–19, <http://www.journalofvision.org/content/13/1/19>, doi:10.1167/13.1.19. [PubMed] [Article]
- Bour, L. J., Aramideh, M., & Ongerboer De Visser, B. W. (2000). Neurophysiological aspects of eye and eyelid movements during blinking in humans. *Journal of Neurophysiology*, *83*(1), 166–176.
- Bour, L. J., de Visser, B. O., Aramideh, M., & Speelman, J. (2002). Origin of eye and eyelid movements during blinking. *Movement Disorders*, *17*(2), 30–32.
- Brindley, G. S. (1962). Two new properties of foveal after-images and a photochemical hypothesis to explain them. *The Journal of Physiology*, *164*(1), 168–179.
- Bristow, D., Haynes, J.-D., Sylvester, R., Frith, C. D., & Rees, G. (2005). Blinking suppresses the neural response to unchanging retinal stimulation. *Current Biology*, *15*(14), 1296–1300, doi:10.1016/j.cub.2005.06.025.
- Burr, D. C. (2005). Vision: In the blink of an eye. *Current Biology*, *15*(14), R554–R556, doi:10.1016/j.cub.2005.07.007.
- Campbell, F. W., & Wurtz, R. H. (1978). Saccadic omission: Why we do not see a grey-out during a saccadic eye movement. *Vision Research*, *18*(10), 1297–1303.
- Coren, S., & Porac, C. (1974). The fading of stabilized images: Eye movements and information processing. *Perception & Psychophysics*, *16*(3), 529–534, doi:10.3758/bf03198582.
- Darwin, R. W., & Darwin, E. (1786). New experiments on the ocular spectra of light and colours. *Philosophical Transactions of the Royal Society of London*, *76*, 313–348, doi:10.2307/106628.
- Daw, N. W. (1962). Why after-images are not seen in normal circumstances. *Nature*, *196*(4860), 1143–1145.
- Evinger, C., Shaw, M. D., Peck, C. K., Manning, K. A., & Baker, R. (1984). Blinking and associated eye movements in humans, guinea pigs, and rabbits. *Journal of Neurophysiology*, *52*(2), 323–339.
- Exner, S. (1890). Das verschwinden der nachbilder bei augenbewegungen [Translation: The disappearance of afterimages during eye movements]. *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, *1*, 47–51.
- Feldman, M., Todman, L., & Bender, M. B. (1974). 'Flight of colours' in lesions of the visual system. *Journal of Neurology, Neurosurgery & Psychiatry*, *37*(11), 1265–1272, doi:10.1136/jnnp.37.11.1265.
- Ferree, C. E. (1908). The intermittence of minimal visual sensations. Studied from the side of the negative after-image. I. The fluctuation of the negative after-image. *The American Journal of Psychology*, *19*(1), 58–129, doi:10.2307/1412824.
- Fiorentini, A., & Mazzantini, L. (1965). Inhibition of after-images due to voluntary eye movements. *Atti della Fondazione Giorgio Ronchi*, *20*(3), 307–320.
- Frederiksen, N. O., & Guilford, J. (1934). Personality traits and fluctuations of the outline cube. *The American Journal of Psychology*, *46*(3), 470–474.
- Friedman, A. H., & Marchese, A. L. (1978). Positive after-image, PAI: Early erasure by saccadic eye movement or Jendrassik manoeuvre. *Cellular and Molecular Life Sciences*, *34*(1), 71–73, doi:10.1007/bf01921909.

- Frisby, J. P. (1980). *Seeing: Illusion, brain and mind*. Oxford, UK: Oxford University Press.
- Gandhi, N. J., & Katnani, H. A. (2011). Interactions of eye and eyelid movements. In S. P. Liversedge, I. Gilchrist, & S. Everling (Eds.), *The Oxford handbook of eye movements* (p. 323). Oxford, UK: Oxford University Press.
- Gerling, J. R., & Spillmann, L. (1987). Duration of visual afterimages on modulated backgrounds: Postreceptor processes. *Vision Research*, *27*(4), 521–527, doi:10.1016/0042-6989(87)90038-1.
- Hazenbergh, S. J., & van Lier, R. (2013). Afterimage watercolors: An exploration of contour-based afterimage filling-in. *Frontiers in Psychology*, *4*, 707, doi:10.3389/fpsyg.2013.00707.
- Helmholtz, H. (1962). *Helmholtz's treatise on physiological optics* (Vol. II). New York: Dover Publications, Inc.
- Ibbotson, M. R., & Cloherty, S. L. (2009). Visual perception: Saccadic omission: Suppression or temporal masking? *Current Biology*, *19*(12), R493–R496.
- Kanai, R., Bahrami, B., & Rees, G. (2010). Human parietal cortex structure predicts individual differences in perceptual rivalry. *Current Biology*, *20*(18), 1626–1630, doi:10.1016/j.cub.2010.07.027.
- Kennard, D. W., Hartmann, R. W., Kraft, D. P., & Boshes, B. (1970). Perceptual suppression of afterimages. *Vision Research*, *10*(7), 575–585, doi:10.1016/0042-6989(70)90051-9.
- Kleinschmidt, A., Sterzer, P., & Rees, G. (2012). Variability of perceptual multistability: From brain state to individual trait. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1591), 988–1000.
- Leigh, R. J., Newman, S. A., Folstein, S. E., Lasker, A. G., & Jensen, B. A. (1983). Abnormal ocular motor control in Huntington's disease. *Neurology*, *33*(10), 1268–1268.
- Leigh, R. J., & Zee, D. S. (1999). *The neurology of eye movements*. New York: Oxford University Press.
- Loftus, G. R., & Masson, M. E. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*(4), 476–490.
- Magnussen, S., & Torjussen, T. (1974). Sustained visual afterimages. *Vision Research*, *14*(8), 743–744, doi:10.1016/0042-6989(74)90074-1.
- Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, *81*(12), 899–917, doi:10.1037/h0037368.
- Matteson, H. H. (1965). After-images observed with intermittent background illumination. *Vision Research*, *5*(4–5), 123–132, doi:10.1016/0042-6989(65)90060-X.
- McLelland, D., Ahmed, B., & Bair, W. (2009). Responses to static visual images in macaque lateral geniculate nucleus: Implications for adaptation, negative afterimages, and visual fading. *Journal of Neuroscience*, *29*(28), 8996–9001, doi:10.1523/jneurosci.0467-09.2009.
- McLelland, D., Baker, P. M., Ahmed, B., & Bair, W. (2010). Neuronal responses during and after the presentation of static visual stimuli in macaque primary visual cortex. *Journal of Neuroscience*, *30*(38), 12619–12631, doi:10.1523/jneurosci.0815-10.2010.
- Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, *10*(7), 903–907. Retrieved from [http://www.nature.com/neuro/journal/v10/n7/suppinfo/nn1917\\_S1.html](http://www.nature.com/neuro/journal/v10/n7/suppinfo/nn1917_S1.html).
- Melcher, D. (2009). Selective attention and the active remapping of object features in trans-saccadic perception. *Vision Research*, *49*(10), 1249–1255, doi:10.1016/j.visres.2008.03.014.
- Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12*(12), 466–473, doi:10.1016/j.tics.2008.09.003.
- Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in human visual cortex. *Journal of Neurophysiology*, *97*(2), 1738–1755, doi:10.1152/jn.00189.2006.
- Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences, USA*, *99*(6), 4026–4031, doi:10.1073/pnas.052379899.
- Powell, G., Bompas, A., & Sumner, P. (2012). Making the incredible credible: Afterimages are modulated by contextual edges more than real stimuli. *Journal of Vision*, *12*(10):17, 1–13, <http://www.journalofvision.org/content/12/10/17>, doi:10.1167/12.10.17. [PubMed] [Article]
- Ridder, W. H., & Tomlinson, A. (1993). Suppression of contrast sensitivity during eyelid blinks. *Vision Research*, *33*(13), 1795–1802, doi:10.1016/0042-6989(93)90170-2.
- Ridder, W. H., & Tomlinson, A. (1997). A comparison of saccadic and blink suppression in normal observers. *Vision Research*, *37*(22), 3171–3179, doi:10.1016/s0042-6989(97)00110-7.
- Robertson, V. M., & Fry, G. A. (1937). After-images observed in complete darkness. *The American Journal of Psychology*, *49*(2), 265–276.

- Schutz, A. C., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2008). Improved visual sensitivity during smooth pursuit eye movements. *Nature Neuroscience*, *11*(10), 1211–1216.
- Scott, A. B., & Collins, C. C. (1973). Division of labor in human extraocular muscle. *Archives of Ophthalmology*, *90*(4), 319.
- Shevell, S. K., St Clair, R., & Hong, S. W. (2008). Misbinding of color to form in afterimages. *Visual Neuroscience*, *25*(3), 355–360, doi:10.1017/S0952523808080085.
- Shimojo, S., Kamitani, Y., & Nishida, S. (2001). Afterimage of perceptually filled-in surface. *Science*, *293*(5535), 1677–1680, doi:10.1126/science.1060161.293/5535/1677 [pii].
- Sperandio, I., Chouinard, P. A., & Goodale, M. A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nature Neuroscience*, *15*(4), 540–542. Retrieved from <http://www.nature.com/neuro/journal/v15/n4/abs/nn.3069.html#supplementary-information>.
- Sylvester, R., Haynes, J.-D., & Rees, G. (2005). Saccades differentially modulate human LGN and V1 responses in the presence and absence of visual stimulation. *Current Biology*, *15*(1), 37–41, doi:10.1016/j.cub.2004.12.061.
- Tolias, A. S., Moore, T., Smirnakis, S. M., Tehovnik, E. J., Siapas, A. G., & Schiller, P. H. (2001). Eye movements modulate visual receptive fields of V4 neurons. *Neuron*, *29*(3), 757–767, doi:10.1016/S0896-6273(01)00250-1.
- van Boxtel, J. J. A., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences, USA*, *107*(19), 8883–8888, doi:10.1073/pnas.0913292107.
- van Lier, R., Vergeer, M., & Anstis, S. (2009). Filling-in afterimage colors between the lines. *Current Biology*, *19*(8), R323–R324, doi:10.1016/j.cub.2009.03.010.
- Volkman, F. C. (1962). Vision during voluntary saccadic eye movements. *Journal of the Optical Society of America*, *52*(5), 571–577.
- Volkman, F. C., Riggs, L. A., Ellicott, A. G., & Moore, R. K. (1982). Measurements of visual suppression during opening, closing and blinking of the eyes. *Vision Research*, *22*(8), 991–996, doi:10.1016/0042-6989(82)90035-9.
- Wade, N. J. (1978). Why do patterned afterimages fluctuate in visibility? *Psychological Bulletin*, *85*(2), 338–352, doi:10.1037/0033-2909.85.2.338.
- Wade, N. J. (2000). *A natural history of vision*. Cambridge, MA: MIT Press.
- Wang, M., Munch, I. C., Hasler, P. W., Prunte, C., & Larsen, M. (2008). Central serous chorioretinopathy. *Acta Ophthalmologica*, *86*(2), 126–145.
- Williams, D. R., & Macleod, D. I. A. (1979). Interchangeable backgrounds for cone afterimages. *Vision Research*, *19*(8), 867–877, doi:10.1016/0042-6989(79)90020-8.
- Wilson, M. H., & Brocklebank, R. W. (1955). Complementary hues of after-images. *Journal of the Optical Society of America*, *45*(4), 293–299.
- Wittenberg, M., Bremmer, F., & Wachtler, T. (2008). Perceptual evidence for saccadic updating of color stimuli. *Journal of Vision*, *8*(14):9, 1–9, <http://www.journalofvision.org/content/8/14/9>, doi:10.1167/8.14.9. [PubMed] [Article]
- Wyatt, H. J. (1998). Detecting saccades with jerk. *Vision Research*, *38*(14), 2147–2153.
- Yarbus, A. (1967). *Eye movements and vision*. New York: Plenum Press.
- Zaidi, Q., Ennis, R., Cao, D., & Lee, B. (2012). Neural locus of color afterimages. *Current Biology: CB*, *22*(3), 220–224.
- Zee, D. S., Chu, F. C., Leigh, R. J., Savino, P. J., Schatz, N. J., Reingold, D. B., & Cogan, D. G. (1983). Blink-saccade synkinesis. *Neurology*, *33*(9), 1233–1233.