Interaction between contours and eye movements in the perception of afterimages: A test of the signal ambiguity theory

Georgie Powell

School of Psychology, Cardiff University, Cardiff, Wales, UK

Petroc Sumner

School of Psychology, Cardiff University, Cardiff, Wales, UK

James J. Harrison

School of Psychology, Cardiff University, Cardiff, Wales, UK

Aline Bompas

School of Psychology, Cardiff University, Cardiff, Wales, UK

An intriguing property of afterimages is that conscious experience can be strong, weak, or absent following identical stimulus adaptation. Previously we suggested that postadaptation retinal signals are inherently ambiguous, and therefore the perception they evoke is strongly influenced by cues that increase or decrease the likelihood that they represent real objects (the signal ambiguity theory). Here we provide a more definitive test of this theory using two cues previously found to influence afterimage perception in opposite ways and plausibly at separate loci of action. However, by manipulating both cues simultaneously, we found that their effects interacted, consistent with the idea that they affect the same process of object interpretation rather than being independent influences. These findings bring contextual influences on afterimages into more general theories of cue combination, and we suggest that afterimage perception should be considered alongside other areas of vision science where cues are found to interact in their influence on perception.

Introduction

Our perception of afterimages seems to depend greatly on the conditions under which they are experienced. This interesting feature renders them an excellent tool to probe the general question of how early sensory signals are interpreted in the light of other available evidence to determine what is perceived and what is not perceived. A curious property of afterimages is that we do not perceive them as frequently—or for as long, as we ought to—based purely on the degree of adaptation. Indeed, if our perception of afterimages correlated perfectly with the adaptation that produces them, we would perceive them very often in the real world, whereas in reality we perceive them rarely. Furthermore, they would not fluctuate in and out of awareness as they often do (Comby, 1909; Wade, 1978). This perceptual instability is reminiscent of the alternating perceptual interpretations observed during binocular rivalry or when viewing bistable figures. Further, the tendency of the visual system to preferentially allow meaningful information to reach awareness is evident in the quick fading of stabilized images that are artefacts of the retina (Coren & Porac, 1974) and our propensity to discount the by-products of lighting conditions such as shadows (Rensink & Cavanagh, 2004).

Afterimages have been studied for over two centuries by philosophers and scientists and they remain of interest to vision researchers today (e.g., Anstis, Geier, & Hudak, 2012; Aristotle, trans. 1910; Bessero & Plant, 2014; Darwin & Darwin, 1786; Hazenberg & van Lier, 2013; Sperandio, Chouinard, & Goodale, 2012; Sperandio, Lak, & Goodale, 2012; van Lier, Vergeer, & Anstis, 2009; Wade, 2000). We now know that they are probably generated from adaptation of cells in early visual pathways (Bachy & Zaidi, 2014; McLelland, Ahmed, & Bair, 2009; Zaidi, Ennis, Cao, & Lee, 2012).

Afterimages can either be of the same or complementary color/luminance to the adapting patch, depending on the intensity of the adapter stimulus and whether the afterimage is viewed in the light or the dark.

Factors such as attention and eye movements during adaptation can influence the resultant perception of afterimages (Bachy & Zaidi, 2014; Lak, 2008; Suzuki & Grabowecky, 2003; van Boxtel, Tsuchiya, & Koch, 2010). However, our interest here is in the perception of afterimage percepts following the adaptation stage. Previous research found afterimage saturation to be increased by surrounding luminance edges (Daw, 1962; van Lier et al., 2009), and we have shown this increase to be greater for afterimages than for real stimuli of similar appearance (Powell, Bompas, & Sumner, 2012). Thus, although the enhancement effect of edges on afterimages and real-colored stimuli likely share some common mechanisms (Francis, 2010; Horwitz, Chichilnisky, & Albright, 2005), the extra enhancement of afterimages suggests that there is something inherently different about postadaptation signals. We also confirmed sporadic reports that saccadic eye movements after the adaptation phase decrease the duration of weak afterimages and reduce the probability of perceiving them at all (Ferree, 1908; Friedman & Marchese, 1978; Helmholtz, 1962; Powell, Sumner, & Bompas, 2015).

One theory—hereafter referred to as the signal ambiguity theory—to explain the effect of these cues is that postadaptation signals are inherently ambiguous because both the temporal properties of the signals and their distribution across cortical areas are not like those from real objects. In line with Bayesian perspectives, we would expect ambiguous signals to be particularly influenced by other information: cues that increase or decrease the likelihood the signal represents a real object (Powell et al., 2012; Powell et al., 2015; also recently echoed by Lupyan, 2015). Surrounding luminance edges may increase the likelihood that the signal is interpreted as a real object rather than as an irrelevant by-product of the visual system because luminance edges often frame the boundaries of real world objects (Fine, MacLeod, & Boynton, 2003; Hansen & Gegenfurtner, 2009; Sharman, McGraw, & Peirce, 2013; Zhou & Mel, 2008). On the other hand, saccadic eye movements may decrease this likelihood because they cause the signal to move around in the world in a way that is unlike a real object. Indeed, afterimages are stabilized on the retina and so their movement during saccades is perfectly correlated with the movement of the eyes, which is unlike the movement of any real world object (Coren & Porac, 1974; Exner, 1890). Relatedly, afterimages will not produce the strong edge-transients that typically occur when the eyes move across a visual scene containing sharp edges (Ennis, Cao, Lee, & Zaidi, 2014), which

could provide further evidence against an afterimage representing a real object.

During real life viewing, the visual scene is usually rich with contextual information and we make saccades several times a second (Findlay & Walker, 1999), so eye movements and inconsistent contours will both be present most of the time; indeed, eye movements will normally be what produce a change in local context (Coren & Porac, 1974). According to the signal ambiguity theory, this would explain why, even though adaptation occurs in everyday viewing, it leads only to rare afterimage experiences. Our only occasional perception of postadaptation signals despite available evidence against them being a real object could be attributed to the fact that calibration to the natural statistics of the world is not always complete (Bompas, Powell, & Sumner, 2013).

However, there are other potential mechanisms that might be sufficient to explain the effect of context and eye movements individually, without the need for the common process described in the ambiguity theory. The contextual influence could be a low-level effect of shared receptive field properties for contours and color in V1 (see Powell et al., 2012 for discussion). On patterned backgrounds, the edge-related activity associated with eye movements (Ennis et al., 2014) may shift the response range of neurons so that the afterimages are more difficult to distinguish from the background. On homogeneous backgrounds, where contextual changes and local edge-related activity are absent, eye movements may affect after images because perception can be biased towards the hue of the postsaccadic location (usually the background gray) via trans-saccadic integration mechanisms (Melcher, 2007; also see Powell et al., 2015 for a full discussion).

Employing the classic approach of testing for interactions, these separate accounts would predict additivity between the two effects (Figure 1C). However, an interaction between the two would suggest that the influence of contours and saccades partly occurs at the same level of visual processing and so would support the signal-ambiguity theory (see Figure 1A, B). To date, the effects of context and eye movements have been studied in isolation; studying how these two cues are combined provides both a more direct test of the signal-ambiguity theory and also brings the study of afterimage perception in line with the wider cue combination literature.

In the present experiments we aimed to test these two hypotheses by measuring afterimage perception during fixation and saccades and in the presence or absence of a luminance contour. Observers reported whether they had seen an afterimage at all, and if they had, they reported its duration. Although previous studies have mainly relied on afterimage duration, this is only valid if the proportions of trials where an afterimage is seen
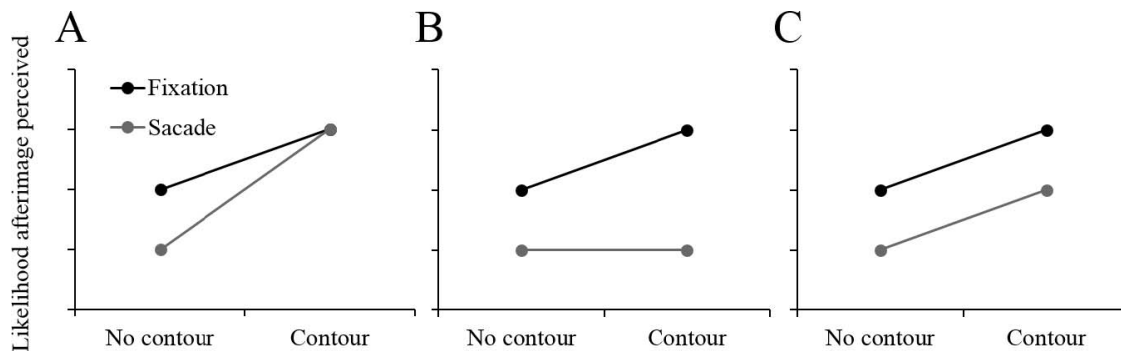
Figure 1. Three predictions for how context (luminance contour) and saccadic eye movements could combine to influence afterimage perception. In (A–B) the contour and saccade cues interact so that the likelihood of perceiving an afterimage is not fully predictable from the effect of each cue in isolation: Their influence is not additive, but interactive. In (A), the saccadic influence is reduced or eradicated by the presence of the contour. The signal ambiguity theory could readily explain this pattern because the correlated movement of the contour and the postadaptation signal provides strong evidence that the signal represents a real object. In (B), the contour effect is reduced or eradicated by the saccade. This could occur simply because the contour is misaligned with the afterimage during saccades due to inaccurate fixation. Alternatively, if the contour is made to be gaze contingent to counteract this problem, its effect may be reduced by the saccade because it now moves "unnaturally" with the eyes, thus producing the opposite effect as in (A). In (C), the effect of the context and the saccades are additive—the contour increases afterimage strength, while the saccade concurrently decreases it. This pattern of results would be expected if the saccade and contour cues exert their influence via completely separate mechanisms.

are comparable across conditions. Furthermore, it could be argued that percentage of afterimages seen is more representative of everyday afterimage experience, because in the real world we often adapt long enough to generate afterimages and yet very rarely see them at all. However, the advantage of using both measures is that we may be able to explore how any interaction might change over time, assuming that the likelihood of afterimage perception reflects the initial representation strength of the afterimage, whereas the duration of the subset of "seen" trials reflects how perception evolves over a longer time frame of a few seconds.

Observers completed the experiment twice, once with short adaptation durations (1.5 s) and again with long adaptation durations (3 s). Pilot studies demonstrated that in order to ensure similar alignment of contours with postadaptation signals in both fixation and eye movement conditions, it was important to employ gaze-contingent contours rather than simply positioning a contour around the expected end point of an instructed saccade.

Methods

Two pilot studies: Luminance edge misalignment during saccades

An initial pilot study suggested that the contour increased afterimage duration less in the saccade condition than in the fixation condition. However, the contour moved with the fixation dot during saccades,

and analysis of the eye movement data revealed greater deviation from the fixation point in the saccade condition than in the fixation condition. This means that the retinal position of the contour, and the extent to which it was aligned with the afterimage, was less accurate in the saccade than in the fixation condition, which would explain the finding. Further, the visual system would expect sharp transients following an eye movement to a new object (Ennis et al., 2014), and afterimage perception may be further hampered if this transient is not aligned with the edges of the afterimage. The importance of contour alignment with the afterimage to produce the contour effect was confirmed in a second pilot experiment, in which we used individual eye movement data from the saccade condition in the first pilot to simulate in the fixation condition the degree of contour misalignment that occurred in the saccade condition. Thus, the contour movement on the retina was now equated in the fixation and saccade conditions. The contour effect was reduced in the fixation condition to the same degree as in the saccade condition.

Therefore, in the main experiment we employed a gaze contingent edge to ensure equally good alignment of the contour with the afterimage in the fixation and saccade conditions. Eye movements were recorded online, and the contour position was continually adjusted so it remained in the center of gaze position. Thus, the only time at which the edge was not aligned with the afterimage in the saccade condition is during the saccade itself. We switched off the contour during these periods, and yoked these durations to insert into future fixation trials. A potential consequence of using a gaze contingent design is

that the contour and the afterimage may be grouped together because they share a common fate—we know that objects that move in synchrony together are grouped together (Wertheimer, 1923). This common fate grouping is likely to be stronger in the saccade condition than the in fixation conditions because fixational jitter is much smaller in amplitude and duration than the larger saccadic eye movements we used, and it is known that common fate grouping is influenced by such factors (Uttal et al., 2000).

Main experiment

Observers

Eight observers (seven naive, one author; five males, three females; average age: 24 years, 3 months) participated. All had normal color vision and normal or corrected-to-normal visual acuity. The observers were all experienced in psychophysical experiments and so followed fixation and eye movement instructions well.

Apparatus

Stimuli were generated by a PC running OpenGL, and presented on a 19 in. Viewsonic P225F monitor (100 Hz refresh rate). Observers were tested in a dark laboratory, and sat at a viewing distance of 70 cm with head movements stabilized using a chin rest. Eye movements were recorded at a rate of 1000 Hz with an Eye Link 2000.

Drift correction

Each observer was calibrated with the eye tracker at the beginning of the experiment. In order to ensure continuous accurate gaze contingency throughout the experiment, a short drift correction was conducted at the beginning of each trial. A red (CIE coordinates: $x = 0.621$, $y = 0.34$, $Y = 5.6$) 0.1° dot placed ±2° from the center of a screen was displayed for 500 ms. If 95% of the eye trace samples within this period were within 0.3° of the mean gaze location, fixation was accepted. Observers were informed with a beep and a 2.5° cross on the screen when fixation was unaccepted, and were required to repeat the procedure until fixation was accepted.

Stimuli and procedure

The trial sequence is shown in Figure 2. Observers completed two sessions of the experiment, one with a short adaptation duration of 1.5 s and another with a longer adaptation duration of 3 s, in order to explore the effect of the cues at two levels of afterimage strength. The order of these sessions was counterbalanced across observers. All stages of the experiment were conducted on a homogenous gray background (CIE coordinates: $x = 0.288$, $y = 0.303$, $Y = 8.5$). Observers first adapted to a pink (CIE coordinates: $x = 0.279$, $y = 0.147$, $Y = 9$) or green (CIE coordinates: $x = 0.289$, $y = 0.609$, $Y = 9$) 3° circle, presented 4° to left or right of center. The adapting colors were therefore equivalent in luminance and saturation and directly opponent in Macleod and Boynton color space. A 0.1° gray dot (CIE coordinates: $x = 0.346$, $y = 0.301$, $Y = 2.7$) was presented in the middle of the adaptation circle to maintain fixation, and this dot remained after the adaptation circle was turned off to begin the afterimage measurement phase. During fixation trials, the dot remained in the same screen location throughout the trial. During saccade trials, the dot alternated between 4° on the left and right of the screen at a frequency of 1.67 Hz. Observers pressed one response key when they perceived that the afterimage had completely faded and a separate response key if they had not seen an afterimage at all.

During the afterimage measurement phase, gaze location was recorded online and on half of the trials a gray (CIE coordinates: $x = 0.289$, $y = 0.302$, $Y = 7.5$) 3° circular contour (0.15° wide) was presented so that it was continually centered on gaze direction (i.e., gaze contingent). Saccades were detected using a speed detector based on the difference between the current and previous eye tracker sample with a velocity criterion of 20°/s. During saccade trials, the contour was not presented during samples that were detected as saccades. During fixation trials, the saccade durations were yoked from the saccade trials and the contour was turned off during these intervals. This method required that the first trial for each observer was always a saccade trial. The contour was turned off during saccades and for saccade-length intervals during fixation to equate saccadic suppression of the contour between fixation and saccade conditions (i.e., by eliminating it in the saccade condition). Trials ended with a 600 ms animated mask consisting of multiple 3° circles randomly changing position and chromaticity at 100 Hz, to reduce carryover effects.

Long and short adaptation sessions were run separately. Within each session, there was a total of four conditions in a 2 (contour present/absent) × 2 (saccade/fixation) within subjects design. Observers received 16 repetitions for each condition in a pseudorandomized order. Adaptation color (green/red) and adaptation side (left/right) were also equated and pseudorandomized across trials.
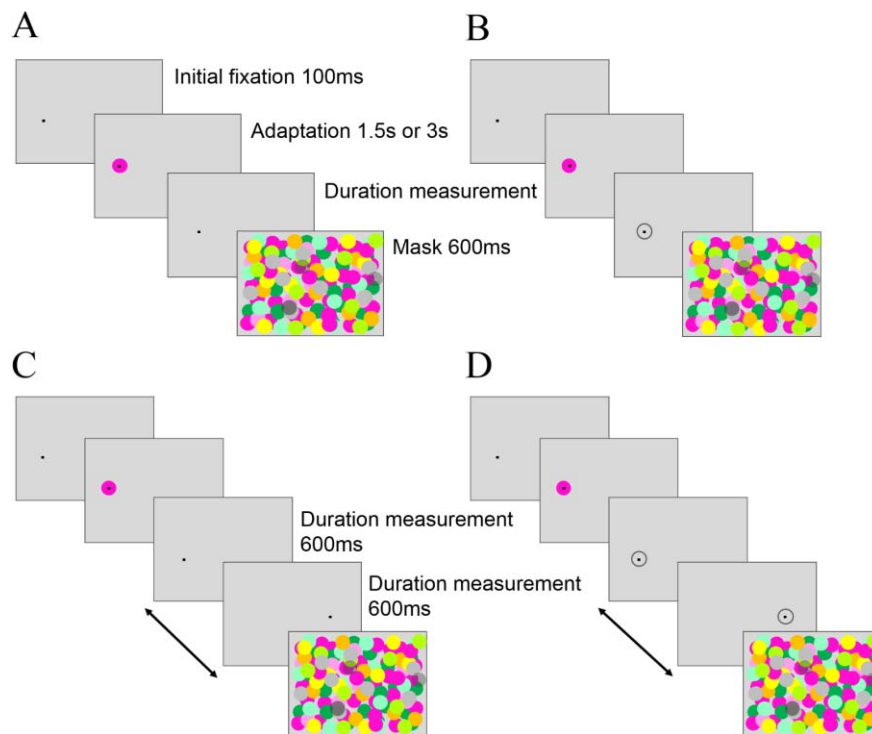
Figure 2. Trial sequences across conditions. (A) Fixation/no contour condition: The observers fixate a colored patch presented on the left or right for either short adaptation (1.5 s) or long adaptation (3 s). The patch is then removed and replaced by a fixation point presented at the same position. The observers indicate when the afterimage has faded or if they had seen an afterimage at all. Following their response, the trial ends with a cycling colored mask to reduce carry over adaptation effects. (B) Fixation/contour condition: Trial sequence runs as in (A), but a luminance contour is presented in the center of gaze position during the duration measurement phase. This contour is contingent on eye position and so moves around to remain in the center of the gaze. The contour is also removed at intervals yoked to the saccade durations in the saccade conditions. (C) Saccade/no contour condition: Trials sequence is the same as the fixation/no contour, but the fixation point jumps to the left and right of the screen at a rate of 1.67 Hz. (D) Saccade/contour condition. Trial is identical to saccade condition/no contour but this time a contour is presented in the center of gaze location when the observers are fixating the dot. The contour is removed for the short interval during the saccades.

Despite drift correcting at the beginning of each trial, the accuracy of the calibration did occasionally slip, resulting in a small displacement of the contour from gaze direction. In order to reduce this shift, an algorithm was employed to carry out a continuous drift correction throughout the trial. When gaze direction was within 2° of the fixation dot, we assumed that the observer was foveating the dot accurately. Therefore, the difference between the sample and the fixation target was assumed to reflect an error between the gaze location and the eye-tracker output. This discrepancy was subtracted from the subsequent sample in order to try and recreate veridical gaze location.

Eye movement analysis

Trials that contained blinks and fixation trials that contained saccades were discarded. Saccades were detected by calculating the "jerk" at each point, which corresponded to the derivative of the eye acceleration (Wyatt, 1998). Samples were recorded as a saccade if the "jerk" value exceeded a criterion of $30°/s^3$. All eye movement traces and the output of the analysis were visually checked. Overall, very few trials were discarded because they contained saccades (less than 5%).

Results and discussion

In two previous studies (Powell et al., 2012, 2015) with the same adaptation patches we found no differences between the pink and green adapting stimuli, and so we collapsed across these trials. Figure 3A and B shows the percentage of trials where an afterimage was seen for both the long (A) and short (B) adaptation sessions. For both saccade and fixation conditions, the contour significantly increased the likelihood of perceiving an afterimage [main effect of contour: long adaptation, $F(1, 7) = 21.09$, $p < 0.01$; short adaptation, $F(1, 7) = 40.20$, $p < 0.001$]. The main
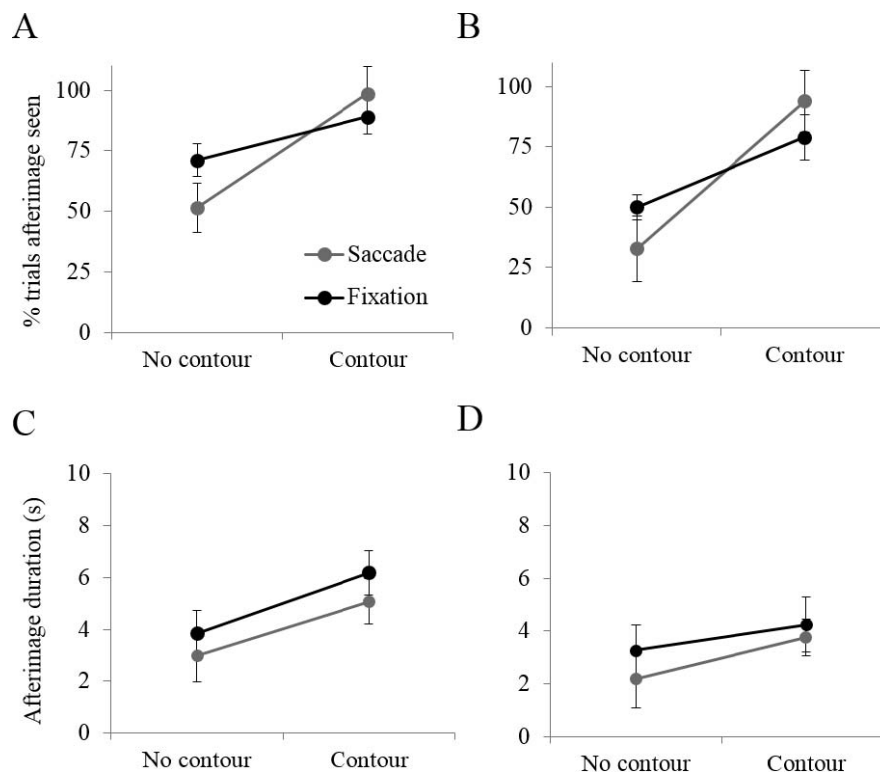
Figure 3. Long adaption (3 s) shown in (A) and (C), short adaptation (1.5 s) shown in (B) and (D). (A–B) The percentage of trials where an afterimage is seen is increased by the contour relatively more in the saccade than the fixation conditions. (C–D) For long adaptation durations, afterimage duration is increased additively by the contour in both fixation (black) and saccade (gray) 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).

effect of saccades was not significant (long adaptation, $p = 0.34$, n.s.; short adaptation, $p = 0.86$, n.s.).

Most importantly, we observed a significant contour × saccade interaction on the percentage of seen afterimages in both long and short adaptation sessions, $F(1, 7) = 20$, $p < 0.01$ and $F(1, 7) = 9.75$, $p < 0.05$, respectively. This interaction, replicated across adaptation durations, is sufficient to support to the idea that the contour and saccade cues are processed together at some level of the visual system. The pattern of results suggests that the presence of a contour eliminates the effect of the saccade cue on afterimage perception (or that the presence of a saccade boosts the contour effect). This pattern could occur if the correlated movement of the contour and the afterimage signal is taken as even stronger evidence that the signal represents a real object.

Figure 3C and D show the perceived duration for long and short adaptation sessions. Note that although all observers perceived at least one afterimage in all conditions, some observers perceived very few afterimages in some conditions (particularly no-contour saccade), making afterimage duration less reliable than the proportion of afterimages seen (which contains all the trials). The contour significantly increased the

average afterimage durations in both the long and short adaptation session [main effect of contour: Figure 3C, long adaptation: $F(1, 7) = 6.45$, $p < 0.05$; Figure 3D, short adaptation: $F(1, 7) = 6.34$, $p < 0.05$] in agreement with previous findings (Powell et al., 2012). Furthermore, saccades significantly reduced the duration of afterimages relative to fixation condition [main effect of saccade: long adaptation: $F(1, 7) = 13.03$, $p < 0.01$; short adaptation $F(1, 7) = 22.45$, $p < 0.05$], which also confirms findings from past research (Powell et al., 2015).

We did not observe a significant contour × saccade interaction on afterimage duration in either the long or short adaptation sessions (long adaptation, $p = 0.50$; short adaptation, $p = 0.52$). This may have been due to removing trials where no afterimages were seen, which as discussed above, were more numerous in some conditions than others. However, replacing the trials where an afterimage was not seen with either the minimum afterimage duration in that condition, or a zero value, and then including these trials in the analysis did not result in a significant contour × saccade interaction either (replaced with minimum afterimage, $p = 0.52$; zero value $p = 0.12$). Normalizing the duration of afterimages on the no-contour fixation

baseline condition did not change the additive pattern either. Taken together, these findings indicate that the difference between the two measures may be genuine and suggests that the nature of the contour/saccade interaction could change over time. Initially, the contour appears to reduce the relative efficiency of the saccade cue to influence afterimage perception and/or the saccade cue boosts the contour effect. After this, the two cues contribute additively to influence how long the afterimage is perceived.

Discussion

Previously we proposed that postadaptation signals may be fundamentally ambiguous because the nature of their responses is different to signals arising from real objects. This ambiguity leads them to be particularly influenced by prior expectations and knowledge about the representation and behavior of real objects—the signal ambiguity theory of afterimage perception (Powell et al., 2012, 2015). The experiments reported here provide a more direct test of this theory by exploring how context and eye movement cues combine to influence afterimage perception. We found an interaction between the cues whereby the effect of saccades was reduced in the presence of a contour, that is, the number of afterimages that were seen became similar for both the saccade and fixation conditions when a contour was also presented. This pattern was replicated for long and short adaptation conditions. This interaction between the cues supports the signal ambiguity theory because it suggests the cues might be processed together at the same level of the visual system.

On the subset of trials on which the afterimage signal was perceived, the contour and saccade effects combined additively. Consistent with previous findings from studying the cues in isolation, the contours increased afterimage perception (Daw, 1962; Powell et al., 2012; van Lier et al., 2009), while the saccades decreased it (Friedman & Marchese, 1978; Kennard, Hartmann, Kraft, & Boshes, 1970; Powell et al., 2015). This suggests that the interaction between the saccade and contour cue may not remain stable over time. Again, a similar pattern was replicated over the two sessions that used different adaptation durations. However, this second conclusion is more tentative, whereas an interaction in one measure is sufficient to support the main conclusion that the two cues influence aftereffects—at least in part—within the same process.

The signal ambiguity theory has recently been echoed by a predictive-coding account of afterimage perception (Lupyan, 2015). In essence, both theories

suggest that prior knowledge and expectations are particularly influential because postadaptation signals are ambiguous. We (Powell et al., 2012) and Lupyan (2015) also both speculate that the source of this ambiguity may lie in the exponential decay of adaptation signals, which creates a neural signal unlike the response to a real object. A further possible reason is that the spatial distribution of signal strengths across the cortex is not alike for real objects and postadaptation signals. Our perspective, therefore, is that afterimages are akin to phenomena such as bistable figures and shadows and reflections, as other examples of how the visual system arrives at perceptual decisions when faced with ambiguous low-level information.

Cue interactions

On the surface, an interaction between the contour and saccade cues could be viewed as surprising given they are likely to be subserved by different systems in the brain. However, it is possible to consider a number of reasons why an interaction might not be unexpected.

In our experiments, the contour (a real object) was gaze contingent and so moved around with the eyes and with the afterimage. The very fact that a real object was moving with the eyes provides evidence against the hypothesis that real objects do not move with the eyes. We, and others (Fiorentini & Mazzantini, 1965), have argued that it is this very hypothesis that explains why saccades reduce afterimage perception. Thus, the relative efficiency of the saccade cue could be reduced by the presence of the contour because the movement of the contour provides evidence that real objects can move with the eyes sometimes. Indeed, the combined movement of the afterimage signal and the contour in the world leads to a stronger interpretation that they are a composite object because they share a "common fate" (Wertheimer, 1923).

Of course, the exact opposite argument could also be predicted—the saccade cue could decrease the efficiency of the contour cue because the contour is now moving unlike a real object (Coren & Porac, 1974). However, the pattern of our results is consistent with the first explanation, which may suggest that the prior for objects surrounded by edges is more influential than the prior for real objects to change retinal positions when the eyes move. Perhaps this is unsurprising given there are examples of when patches of color remain fixed on the retina across eye movements, for example during smooth pursuit, when saccading across a large uniform object, or when saccading between two objects of similar appearance.

These explanations could help us to understand why initially the contour cue has more of an influence over

after image perception than the saccade cue. However, for our longer term duration measure we found an additive pattern of contour and saccade effects. Why might the cue interaction change over time? One tentative posthoc explanation could be that the saccade cue builds up over time as more saccades are performed, and the evidence accumulates that the afterimage signal does not behave like a real object.

One possible alternative explanation that could be suggested is that the two processes occur separately and sequentially if eye movements only influence weak afterimages. If the contour acts first to change the strength of the afterimage signal, and then the eye movement influences weak signals more than strong ones, this condition could produce a pattern like the interaction we observe. However, this would also predict a different effect of eye movements in the short and long adaptation sessions that generated weak and strong afterimages respectably, and this we did not observe. Indeed, the likelihood of perceiving an afterimage in the long adaptation condition *without* a contour was similar to the likelihood of perceiving an afterimage in the short adaptation condition *with* a contour (compare Figure 3A and B); however, the effect of saccades is clearly different between the two. Therefore, although we cannot definitely reject this possibility, we have no evidence to support the idea that the effect of eye movements is driven by signal strength alone, and the most likely explanation for the behavioral interaction remains that there is a processing interaction between the cues.

A possible methodological explanation for our findings is that the contour flashing on and off in the fixation condition led to a reduction in the contour effect during fixation. We introduced this to mimic periods during a saccade where saccadic suppression will reduce intensity of the contour representation, and the actual onsets and offsets were yoked from saccade trials for each participant. This explanation seems unlikely, however, because it would be more likely to predict an interaction in the duration measure, where more flashes occur, than in the number of afterimages seen. Further, pilot studies revealed that the contour effect is reduced in the saccade condition relative to the fixation condition if the degree of contour alignment is not equated between the conditions. A possible reason for this is that the visual system expects sharp transients following eye movements (Ennis et al., 2014) and these would not occur for an afterimage on its own. When the contour and the afterimage are perfectly aligned (i.e., contour is gaze-contingent), sharp transients will be produced by the composite contour-afterimage signals. However, when the afterimage is misaligned with the contour, the contour will produce transients but the afterimage will not, thus potentially providing another cue that the afterimage is illusory.

Other factors that influence afterimage perception not studied here

We have studied two key influences on afterimage perception, but there are likely other factors that are also important, particularly during natural viewing. For example, there will be additional effects when eye movements occur on patterned backgrounds than on the homogenous gray backgrounds that we used in the present experiments. Stationary edges in the scene will cause transient activity (Ennis et al., 2014) and may shift the responses of neurons to a range where the edges of the afterimage are more difficult to distinguish from the background. If this effect is much more transient than the adaptation underlying an afterimage, then this could explain why after images are sometimes reported to re-emerge gradually following a saccade. Saccades on patterned backgrounds will also change the local contours around the afterimage, and thus be the cause of a contour effect. This could explain reports that afterimage perception can be "refreshed" if gaze is directed back to the original location (Daw, 1962).

Furthermore, we may not perceive afterimages most of the time because we simply do not attend to them although, somewhat counterintuitively, attention towards an afterimage has been shown to reduce its duration (Lou, 2001). Tse, Kohler, and Reavis (2010) demonstrated that perception of two afterimage patterns that are superimposed in a rectangular-cross formation and surrounded by their own framing perpendicular contours, will alternate (or "rival") based on which contour attention is directed towards. This suggests that attention towards the surrounding context is more important in determining afterimage perception than attention towards the afterimage itself. Note we do not expect that attention could have influenced our findings because if attention were to have an effect, it would actually be in the opposite direction to the one we observed. If we assume less attention towards the afterimage and contour in the saccade conditions (because attention moves before the saccade), then an attention explanation predicts that afterimage perception is enhanced during saccades relative to fixation and that the contour cue during saccades is less effective.

Objects and contours: An art history perspective

A perceptive reviewer asked us to consider why expressionist artists tended to demarcate the objects in their paintings with dark contours. The work of Paul

Figure 4. *Still Life with Apples and Peaches*, Paul Cezanne, c.1905. Reprinted from the National Gallery of Art, Open Access.

Cézanne is an excellent example of this (Figure 4). The thick, dark contours surrounding the peaches and apples create an impression of intensified solidity. One might infer from this that Cézanne understood, at least implicitly, the statistical frequency of sharp luminance edges surrounding objects and our visual system's tendency to prioritize them, and sought to amplify them for artistic effect. In other words, he may have been working with a theory akin to the signal ambiguity theory addressed in this paper: Objects without clear edges will be perceived less strongly or as less real; if you want the visual system to perceive an object strongly, emphasize its edge. Note, artists such as Cézanne did not just use strong contours to exaggerate the solidity of shapes, they also utilized color contrast: The edges surrounding the orange peaches are tinged blue. What would such an artist's representation of an afterimage be? We speculate they would be merged into the colorful swirls of a van Gogh sky rather than demarcated by thick contours on a Cézanne tabletop. Furthermore, based on Ennis et al. (2014), we would expect these types of painting to elicit very strong transient responses as the eye moves over the contours, which is perhaps a mechanism through which the visual experience is boosted.

Conclusion

We explored how luminance edges and saccadic eye movements influence the perception of afterimages when both are present. Our results indicated that at first the two cues interact. Later the two cues appeared to be combined additively—the contour increased afterimage duration by around the same amount as the saccadic eye movements decreased it. The presence of an interaction between the two cues suggests that they do not operate independently and are in part processed at the same level of the visual system. These findings place the study of afterimage perception within the wider cue integration literature. Our novel perspective is that afterimages should sit beside other topics of study such as depth perception, bistable percepts, and perceptual constancies (e.g., color constancy and lightness constancy) as tools to probe how the visual systems comes to perceptual decisions in the face of ambiguous information.

Keywords: afterimages, eye movements, context, conscious awareness

References

Anstis, S., Geier, J., & Hudak, M. (2012). Afterimages from unseen stimuli. *i-Perception*, *3*(8), 499.

Aristotle (1910). *The works of Aristotle* (Vol. 3; W. D. Ross, & J. A. Smith, trans.). Oxford, UK: Clarendon Press.

Bachy, R., & Zaidi, Q. (2014). Factors governing the speed of color adaptation in foveal versus peripheral vision. *Journal of the Optical Society of America A*, *31*(4), A220–A225.

Bessero, A.-C., & Plant, G. T. (2014). Should 'visual snow' and persistence of after-images be recognised as a new visual syndrome? *Journal of Neurology, Neurosurgery & Psychiatry*, doi:10.1136/jnnp-2013-306827.

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, doi:10.1167/13.1.19. [PubMed] [Article]

Comby, J. H. (1909). The intermittence of minimal visual sensations. I. The fluctuation of the negative after-image. *Psychological Bulletin*, 6(9), 305–307, doi:10.1037/h0063993.

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. By Robert Waring Darwin, M. D.; communicated by Erasmus Darwin, M. D. F. R. S. *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, doi.org/10.1038/1961143a0.

Ennis, R., Cao, D., Lee, B. B., & Zaidi, Q. (2014). Eye movements and the neural basis of context effects on visual sensitivity. *The Journal of Neuroscience, 34*(24), 8119–8129.

Exner, S. (1890). Das verschwinden der nachbilder bei augenbewegungen [Translation: The disappearance of afterimages in eye movements]. *Zeitschrift fur Psychologie und Physiologie der Sinnesorgane, 1*, 47–51.

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.

Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences, 22*(04), 661–674.

Fine, I., MacLeod, D. I. A., & Boynton, G. M. (2003). Surface segmentation based on the luminance and color statistics of natural scenes. *Journal of the Optical Society of America, 20*(7), 1283–1291. Retrieved from http://josaa.osa.org/abstract.cfm?URI=josaa-20-7-1283

Fiorentini, A., & Mazzantini, L. (1965). Inhibition of after-images due to voluntary eye movements. *Atti della Fondazione Giorgio Ronchi, 20*(3), 307–320.

Francis, G. (2010). Modeling filling-in of afterimages. *Attention, Perception & Psychophysics, 72*(1), 19–22, doi:72/1/19 [pii] 10.3758/app.72.1.19.

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.

Hansen, T., & Gegenfurtner, K. R. (2009). Independence of color and luminance edges in natural scenes. *Visual Neuroscience, 26*(01), 35–49, doi:10.1017/S0952523808080796.

Hazenberg, S. J., & van Lier, R. (2013). Afterimage watercolors: An exploration of contour-based afterimage filling-in. *Frontiers in Psychology, 4*, 701.

Helmholtz, H. (1962). *Helmholtz's treatise on physiological optics* (Vol. II). New York, NY: Dover Publications, Inc.

Horwitz, G. D., Chichilnisky, E. J., & Albright, T. D. (2005). Blue-yellow signals are enhanced by spatiotemporal luminance contrast in Macaque V1. *Journal of Neurophysiology, 93*(4), 2263–2278, doi:10.1152/jn.00743.2004.

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.

Lak, A. (2008). Attention during adaptation weakens negative afterimages of perceptually color-spread surfaces. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale, 62*(2), 101–109.

Loftus, G. R., & Masson, M. E. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review, 1*(4), 476–490.

Lou, L. (2001). Effects of voluntary attention on structured afterimages. *Perception, 30*(12), 1439–1448. Retrieved from http://www.perceptionweb.com/abstract.cgi?id=p3127

Lupyan, G. (2015). Object knowledge changes visual appearance: Semantic effects on color afterimages. *Acta Psychologica, 161*, 117–130, doi:10.1016/j.actpsy.2015.08.006.

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.

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

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, doi:10.1167/12.10.17. [PubMed] [Article]

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, 1–13, doi:10.1167/15.3.20. [PubMed] [Article]

Rensink, R. A., & Cavanagh, P. (2004). The influence of cast shadows on visual search. *Perception*, *33*(11), 1339–1358.

Sharman, R. J., McGraw, P. V., & Peirce, J. W. (2013). Luminance cues constrain chromatic blur discrimination in natural scene stimuli. *Journal of Vision*, *13*(4):14, 1–10, doi:10.1167/13.4.14. [PubMed] [Article]

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, doi.org/10.1038/nn.3069.

Sperandio, I., Lak, A., & Goodale, M. A. (2012). Afterimage size is modulated by size-contrast illusions. *Journal of Vision*, *12*(2):18, 1–10, doi:10.1167/12.2.18. [PubMed] [Article]

Suzuki, S., & Grabowecky, M. (2003). Attention during adaptation weakens negative afterimages. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(4), 793–807. Retrieved from http://www.sciencedirect.com/science/article/B6X08-49FPG0V-5/2/0aee73b1aee179bc8bf768f1031f0e5a

Tse, P., Kohler, P., & Reavis, E. (2010). Attention modulates perceptual rivalry within after-images. *Journal of Vision*, *10*(7): 194, doi:10.1167/10.7.194. [Abstract]

Uttal, W. R., Spillmann, L., Stürzel, F., & Sekuler, A. B. (2000). Motion and shape in common fate. *Vision Research*, *40*(3), 301–310.

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.

Wade, N. J. (1978). Why do patterned afterimages fluctuate in visibility? *Psychological Bulletin*, *85*(2), 338–35, doi:10.1037/0033-2909.85.2.338.

Wade, N. J. (2000). *A natural history of vision*. Cambridge, MA: MIT Press.

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II [Translation: Laws of organization in perceptual forms. A source book of Gestalt psychology]. *Psycologische Forschung*, *4*, 301–350.

Wyatt, H. J. (1998). Detecting saccades with jerk. *Vision Research*, *38*(14), 2147–2153.

Zaidi, Q., Ennis, R., Cao, D., & Lee, B. (2012). Neural locus of color afterimages. *Current Biology: CB*, *22*(3), 220–224. Retrieved from http://linkinghub.elsevier.com/retrieve/pii/S0960982211013984

Zhou, C., & Mel, B. W. (2008). Cue combination and color edge detection in natural scenes. *Journal of Vision*, *8*(4):4, 1–25, doi:10.1167/8.4.4. [PubMed] [Article]