Rivalry between afterimages and real images: The influence of the percept and the eye

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In binocular rivalry, the conscious percept alternates stochastically between two images shown to the two eyes. Both suppressed and dominant images form afterimages (AIs) whose strength depends on the perceptual state during induction. Counterintuitively, when these two AIs rival, the AI of the previously suppressed percept gains initial dominance, even when it is weaker. Here, we examined rivalry between afterimages, between real images, and between both to examine eye-based and binocular contributions to this effect. In all experiments, we found that for both AIs and real images, the suppressed percept consistently gained initial dominance following a long suppression period. Dominance reversals failed to occur following short suppression periods and depended on an abrupt change (removal) of the stimulus. With real images, results were replicated also when eye channels were exchanged during the abrupt change. The initial dominance of the weaker, previously suppressed percept is thus not due to its weaker contrast, to it being an afterimage, or to monocular adaptation effects as previously suggested. Instead, it is due to binocular, higher level effects that favor a perceptual switch after prolonged dominance. We discuss a plausible neural account for these findings in terms of neural interactions between binocular and eye-related stages.

Keywords: afterimages, binocular rivalry, flash suppression, feedback, masking, adaptation


Introduction

When distinct stimuli are presented to each eye, conscious perception tends to alternate stochastically between the two, a phenomenon termed binocular rivalry. The origins of these perceptual switches are still under debate, but most likely they are not due to an isolated competition between monocular channels, nor are they due purely to high-level effects, but to neural interactions involving several neural sites (Blake & Logothetis, 2002). Negative afterimages of oriented gratings are perceived through the adapted eye only, which is why they are believed to be early monocular phenomena, induced, e.g., by adaptation at retinal or early visual eye-based neural stimulus representations (Craik, 1940; Kelly & Martinez-Uriegas, 1993; Shimojo, Kamitani, & Nishida, 2001; Wilson, 1997). When two gratings are presented dichoptically in rivalry such that one is suppressed and one visible (dominant), both form an afterimage. Interestingly, AI formation is affected by perceptual competition, in that the AI of a perceptually suppressed image has been reported to be weaker (and in some cases stronger) than AIs formed without perceptual competition (Brascamp, van Boxtel, Knapen, & Blake, 2010; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005). Therefore, the monocular or eye-based stimulus representations involved in AI formation must somehow be affected by the mechanisms involved in perceptual suppression.
In accord with this, one interpretation of the differential AI formation during rivalry was that the eye-related neural population coding for the dominant stimulus may be more active and therefore also adapt more during dominance, thus leading to a stronger AI formation (Gilroy & Blake, 2005). This would require a markedly differential activity in monocular neural populations during rivalry, as has been hypothesized in a theoretical study (Blake, 1989).

However, this model is difficult to reconcile with electrophysiology showing that neural spiking activity of monocular neurons (we use this term somewhat loosely here, including neurons with strong response bias to one eye) during rivalry is only minimally or not at all modulated by the perceptual state—dominant or suppressed stimuli are virtually indistinguishable in terms of spiking activity of neurons in LGN and V1 (Gail, Brinksmeyer, & Eckhorn, 2004; Lehky & Maunsell, 1996; Leopold & Logothetis, 1996; Wilke, Logothetis, & Leopold, 2006). Interestingly, Gilroy and Blake (2005) found that after induction of differential AIs by one high-contrast dominant stimulus and one low-contrast suppressed stimulus, it was the (weaker) AI of the previously suppressed stimulus that gained initial dominance once the real stimuli were removed.

This result is, at first sight, counterintuitive for several reasons: First, stronger stimuli tend to gain initial dominance in rivalry (Levett, 1966). Second, attended stimuli—like the previously dominant one—tend to gain initial dominance (Mitchell, Stoner, & Reynolds, 2004). Lastly, previous studies indicated a strong monocular stabilizing effect in dominance. In other words, once a given eye mediates the dominant percept, it tends to remain dominant, even when another stimulus is shown to it (Blake, Westendorf, & Overton, 1980). More recent studies have, however, shown that this effect depends on the dominance time prior to presentation of the new stimulus (Bartels & Logothetis, 2010). Despite this, it was the AI originating from the suppressed eye that gained dominance (Gilroy & Blake, 2005).

In the present study, we therefore sought to find experimental evidence supporting alternative interpretations for the initial dominance of the AI originating from the previously suppressed stimulus (and eye). We therefore asked the question on whether the observed effect was specific to afterimages or not and whether it depended on monocular channels—if not, one can exclude differential neural adaptation of eye-based channels as its cause. We also wanted to know whether the reasoning we were drawn to by an entirely different previous study may account for the counterintuitive AI finding reported above.

In our previous study, we used brief stimulus disruptions to probe perceptual stability as a function of time and monocular channel (Bartels & Logothetis, 2010). Two effects were revealed to occur during perceptual dominance of one stimulus. First, there was a relatively strong eye-based stabilizing contribution that tended to maintain dominance of a given eye (regardless of the stimulus) that weakened over time toward the end of a dominance period. Second, a stimulus-based (binocular) effect stabilized a given percept at the beginning of a dominance period and weakened over time, eventually destabilizing the percept, making a perceptual switch more likely. In that study, we found that a stimulus disruption (i.e., presentation of a binocular pattern for 100 ms) after only a few hundred milliseconds of dominance did not lead to a change in dominance—the dominant eye remained dominant. However, a stimulus disruption after several seconds of stable dominance tended to induce a perceptual switch. This latter effect in turn is likely directly related to a classic effect termed flash suppression (Wolfe, 1984). Flash suppression essentially describes the phenomenon that a disruption or removal of stimuli can lead to a dominance reversal (Wolfe, 1984). In present-day experiments, it is frequently used to induce dominance in one eye by the sudden presentation of a new stimulus to that eye. Our hypothesis here is that a removal of real images after several seconds, as done in AI experiments, may thus induce a dominance reversal due to exactly this effect. This dominance reversal in turn is a high-level effect, as what reverses is the percept, regardless of the eye of origin (Bartels & Logothetis, 2010).

Here, we first replicated the previous findings on AI rivalry of Gilroy and Blake (2005), showing that after removal of real images the weaker AI of the previously suppressed eye initially dominates. We then also tested whether indeed the AI of the previously suppressed stimulus was weaker compared to the AI of the previously dominant stimulus. In a third experiment, we replaced one AI by a weak-contrast version of its inducing real image. The same effect was found—no matter whether the previously dominant or suppressed AI was replaced by a real image, it was the previously suppressed percept that gained initial dominance, regardless whether it was a real image or an AI. In a fourth experiment, we removed the real gratings that induced the AIs gradually instead of abruptly and found that the effect reversed: now the AI of the previously dominant image tended to gain initial dominance, indicating that the abruptness had accounted for the dominance reversal. Finally, we found that even when full-contrast images were presented instead of AIs but preceded by a brief binocular mask mimicking the stimulus disruption of removing the real images, the previously suppressed grating dominated. This was the case even when the stimuli were exchanged between the eyes, indicating that the dominance reversal is a higher level effect, independent of the eye of origin. Dominance reversal failed to occur reliably when the preceding dominance duration was short also in AI rivalry, indicating that AI dominance reversal, like real stimulus dominance reversal, is time-dependent.

Therefore, we conclude that perceptual switches after prolonged dominance periods are primarily due to some higher level influence, and not primarily due to monocular adaptation, and can thus be accounted for by the general effect of flash suppression and by its binocular and
time-dependent component presented in our previous study (Bartels & Logothetis, 2010; Wolfe, 1984). We discuss the results also in context of potential reasons that may account for the differential AI formation during perceptual rivalry.

**General methods**

**Subjects and stimuli**

Three types of binocular rivalry experiments were conducted: (a) rivalry between afterimages (AIs); Experiments 1, 2, and 4; (b) rivalry between an AI and a real image (in two variations): Experiment 3; and (c) rivalry between real images following a brief stimulus disruption: Experiment 5. Six to eight subjects (see figures) participated in each experiment (half males, half females). They were aged between 24 and 34 years and had normal or corrected-to-normal vision. All gave written informed consent, and the experiments were approved by the Joint Ethics Committee of the Max Planck Institute and of the University Clinic Tübingen. In each experiment, all but two participants were naïve with regard to the purpose of the experiment, and all were well trained on binocular rivalry paradigms. Stimuli were presented on two linearized monitors facing each other (width: 41 cm, resolution $1024 \times 768$ at 85 Hz) and were viewed through a set of angled silver-coated mirrors at a distance of 118 cm. Stimuli were generated using Cogent 1.29 (John Romaya, Wellcome Department of Imaging Neuroscience, University College London, www.vislab.ucl.ac.uk/CogentGraphics.html) on a Windows PC running Matlab 2006b (Mathworks). All stimuli were presented on a black ($0 \text{ cd/m}^2$) background with a central fixation cross (0.22 deg) and were superimposed on a gray (4 or 8 cd/m$^2$) CIE chromaticity: $x = 0.262, y = 0.291$) circular annulus (3 deg) containing a black concentric circle (2-deg diameter, 0.04-deg thickness) and centrifugal cross-hairs that aided binocular fusion. Prior to data collection, subjects were accustomed to rivalry by a few trial sessions of AI rivalry (Experiment 1) and a few 3-min rivalry sessions using the same stimuli. In spontaneous rivalry, the mean dominance time of the stimuli was approximately 2–3 s.

**Rivalry between AIs**

The first two experiments were performed to confirm and extend the findings of Gilroy and Blake (2005) and followed their Experiment 3. AIs were induced using a dominant stimulus and a suppressed stimulus, and the first question is which AI dominates after removal of the initial stimuli. The second question is whether the AI of the previously suppressed stimulus or that of the previously dominant stimulus is stronger. Gilroy and Blake assumed, but did not directly test, that the AI of the previously dominant stimulus was stronger. We tested this here explicitly because of recent reports that, in certain circumstances, the opposite can be true (Brascamp et al., 2010).

**Methods**

Two experiments were performed, using distinct sets of volunteers and using slightly varied stimulus parameters. In Experiment 1, AI dominances were measured. In Experiment 2, AI dominances and also relative AI strengths were measured.

**Experiment 1** (see Figure 1a): First, a flash suppression paradigm induced dominance of one stimulus: one half-luminance sinusoidal grating was presented to one eye for 500 ms, followed by the additional presentation of another, orthogonal full-luminance grating to the other eye (this stimulus now being dominant; Wolfe, 1984; see Figure 1a). Gratings had 1.4-deg diameter, 3.6 cpd, 100% contrast, and 6.5 and 13 cd/m$^2$ luminance, respectively. Then, after 3000-ms AI induction by these two stimuli, both gratings were removed from the gray background to reveal the two AIs of each eye, which engaged in rivalry for 3 s. The AI induction time of 3 s was used, as during spontaneous rivalry sessions preceding the experimental trials, the mean reversal rate for these stimuli was around 3 s.

Subjects indicated by pressing one of two buttons which of the two AI orientations gained initial dominance after removal of the real stimuli. They pressed no button to indicate a failed trial when dominance induction by flash suppression had failed, when a spontaneous switch had occurred prior to removal of the gratings, or when no clear AI dominance occurred. After presentation of 6 s of a white noise pattern (100% contrast, luminance: 6.5 cd/m$^2$) and 2 s of gray background, the next trial started. Each subject performed at least four blocks of 16 trials each. In each block, trials were counterbalanced such that dominance was induced equally often in each eye and that left/right-orientated gratings were equally often dominant in each eye, with trials presented in a pseudorandom sequence.

**Experiment 2** (see Figure 2a): The same paradigm was applied as in Experiment 1, with the following differences. Flash suppression induced dominance by presenting a first grating of 60% contrast for 300 ms to one eye, followed by the additional presentation of the orthogonal stimulus of 100% contrast to the other eye for 2000 ms. The AI induction time of 2 s was used here, as during spontaneous rivalry sessions preceding the experimental trials, the mean reversal rate for these stimuli was around 2 s. In this experiment, all gratings were isoluminant (as in Gilroy &
Blake, 2005), with the following parameters: 1.6-deg diameter, 1.9 cpd, and luminance of 8.3 cd/m², presented on a gray isoluminant background.

As in Experiment 1, after removal of both stimuli, one of the two AIs gained immediate dominance in most trials. In order to obtain a relative measure of AI strengths, we presented two gratings of vertical orientation and with 12% and 18% contrast, respectively, to the top and bottom of the perceived AI, 1 s after removal of the AI-inducing gratings (see Figure 2a). Subjects had the dual task of indicating which of the two AI orientations had gained initial dominance (with the same instructions as in Experiment 1), followed by the 2-alternative forced-choice task to indicate which of the two vertical gratings matched the perceived strength of the AI better. The contrasts of the vertical strength-matching gratings had

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![Figure 1](image1.png)

Figure 1. Rivalry between afterimages (AIs). (a) A flash-suppression paradigm was used to induce dominance of the second presented grating. After 3 s of stable dominance, both gratings were removed and subjects reported the orientation of the initially dominant AI. (b) Percentages of AI dominance of the previously suppressed grating (sups) or the previously dominant grating (doms; only successful trials considered, such that both sum to 100%). The AI of the previously suppressed grating was more likely to gain initial dominance (t-test: p < 0.00002, n = 7 subjects). Fails: percentage of failed trials (see Methods section). LE/RE: left/right eye. Error bars: SEM across 7 subjects.

![Figure 2](image2.png)

Figure 2. Rivalry between AIs and relative strengths of perceived AIs. (a) Similar procedure as in Experiment 1, with the additional presentation of two weak-contrast vertical gratings 1 s after removal of the AI-inducing gratings. The two weak-contrast gratings were presented above and below the AI (partially overlapping the AI). Subjects then reported the orientation of the perceived AI and whether the strength of the AI matched better the weaker or stronger vertical grating. (b) Percentages of AI dominance of the previously suppressed grating (sups) or the previously dominant grating (doms; only successful trials considered, such that both sum to 100%). The AI of the previously suppressed grating was more likely to gain initial dominance (t-test: p = 0.022, n = 8 subjects). (c) Percentage of trials in which the AI was perceived more similar to the weaker contrast (compared to the stronger contrast) vertical grating, shown for cases when the AI of the previously suppressed or dominant grating was perceived. AIs of the previously suppressed grating were more often perceived weaker than those of the previously dominant grating (p = 0.031, n = 8). Error bars: SEM across 8 subjects.
been determined empirically (by author AB) during test runs to yield a good match to the perceived AI strengths of the suppressed and dominant gratings. Each of the eight subjects performed 8 blocks of 8 counterbalanced trials.

Results

Figure 1b shows the results of Experiment 1. Indeed, the AI of the previously suppressed stimulus was consistently more likely to gain initial dominance, in 72 ± 5.4% (mean ± SD) of trials (t-test: p < 0.00002, n = 7 subjects). This was observed in each of the seven subjects individually (with at least p < 0.02). The results therefore replicate those obtained in the initial study (Gilroy & Blake, 2005).

Figures 2b and 2c show the results from Experiment 2. Figure 2b also shows that in this experiment with 8 different subjects and somewhat different stimulus parameters, the AI of the previously suppressed grating was more likely to gain initial dominance, even though with less overwhelming frequency than in Experiment 1 or compared to the results (obtained in 4 subjects) of Gilroy and Blake (2005), with 58.4 ± 9.7% (mean ± SD) of the trials (t-test: t(7) = 2.46, p = 0.022, n = 8 subjects). Figure 2c shows that, as assumed by Gilroy and Blake, indeed the AI of the previously suppressed grating was more frequently judged similar to the weak-contrast grating (in 75.0 ± 27.6% (mean ± SD) of the trials) than the AI of the previously dominant grating (in 42.5 ± 31.8% of trials; t-test: t(7) = 2.21, p = 0.031, n = 8).

Conclusion

The results first confirmed the prior, counterintuitive finding that in AI rivalry, the AI of the previously suppressed stimulus tends to gain initial dominance. Second, the results show that the AI of the previously suppressed grating was indeed perceived as weaker in contrast than the AI of the previously dominant stimulus, as hypothesized by Gilroy and Blake (2005). This renders the first finding even more puzzling: why should a relatively weaker AI of a stimulus that was suppressed gain initial dominance after removal of the AI-inducing stimuli?

Methods

This second set of experiments was identical to Experiment 1, but after AI induction only one of the two initial gratings was removed, while the other was reduced in contrast to a low level that matched perceptually AI intensity. The intensity adjustment was performed empirically in monocular experiments, by iteratively increasing contrast until the subject perceived the real low-contrast grating and not the AI of the inducing full-contrast grating.

There were two sub-experiments in which either the suppressed grating was removed (leaving the AI of the suppressed grating) and the dominant grating was replaced by a low-contrast (AI-mimicking) grating or vice versa. Trials of both sub-experiments were presented in random sequence within the same block. According to the subject’s reports (including the author’s experience), one could not tell whether one perceived an AI or a low-contrast real image, and thus, one could also not tell the trial types apart. As in Experiment 1, subjects pressed one of two buttons to indicate the perceived orientation after removal of the high-contrast gratings. In addition, subjects pressed one of two additional buttons to indicate the perceived phase of the grating: one button if luminance was low, the other if luminance was high behind the fixation cross. This second button press allowed us to determine whether subjects perceived the AI (inverted phase compared to the initial grating) instead of the low-contrast AI-mimicking grating (same phase as the initial grating) in trials where the perceived orientation matched that of the low-contrast AI-mimicking grating. Note that, subjectively, the change in phase was barely noticeable, as the change in orientation was more salient. Compared to Experiment 1, all gratings had a lower spatial frequency of 1.4 cpd and an increased width of 2.2 deg, which made it easier to perceive the grating phase. The low-contrast AI-mimicking gratings were isoluminant to the gray background (4 cd/m²) and had a mean contrast of 52 ± 18% (mean ± SD) across the six subjects. Note that this grating had to “override” the underlying AI. When the eye became dominant in which the low-contrast AI-mimicking grating was shown, subjects perceived reliably the shown grating rather than the AI. The few trials in which subjects perceived the AI instead of the real grating shown to the same eye are excluded from the main analysis and indicated by “err” next to the “fails” in Figure 3. Subjects performed at least 5 blocks of 16 trials each.

Results

The results show that in both situations the previously suppressed orientation—phase inverted or not, i.e., AI or
real—was more likely to gain initial dominance. In average, subjects perceived in 77 ± 9.6% (mean ± SD) of trials the low-contrast physical version of the previously suppressed grating as dominant over the AI of the previously dominant grating (t-test: $p < 0.0005$, $n = 6$ subjects; $p < 0.005$ in each subject), and they perceived in 74 ± 15.2% (mean ± SD) of trials the AI of the previously suppressed grating as dominant over the low-contrast physical version of the previously dominant grating ($p < 0.0006$ and $p < 0.006$, respectively, across $n = 6$ subjects). Fails: percent failed trials, err: percent trials where the AI instead of the real grating of the same orientation was perceived (based on phase reports). Error bars: SEM across 6 subjects.

**Conclusion**

Subjects reported the previously suppressed orientation as initially dominant, no matter whether this was an AI or an AI-mimicking real image. This experiment ruled out that the phase inversion between real image and afterimage, or inherent properties unique to AIs may account for the initial result of Experiment 1. However, it should be noted that the strength of the AI relative to that of its competing low-contrast real grating was matched only in monocular experiments prior to the rivalry experiments, but that their relative strengths during the dichoptic experiments are unknown. We cannot, therefore, fully rule out that the present results may have been influenced by strength differences. However, these would be unlikely to have strongly biased the results, as in both experiments the same outcome occurred, with the previously suppressed grating gaining initial dominance, no matter whether this was an AI or a real grating. In addition, subjectively, no strength differences were apparent to the subjects (including the authors) in this experiment. In Experiments 1 and 2, strength differences were perceived and measured, yet did not determine the outcome, thus making it unlikely that this was the case here.

The present results therefore suggest that there is no inherent advantage to either AI or real image in gaining dominance, as in one sub-experiment consistently the AI, and in the other consistently the real image, gained dominance—whichever orientation was suppressed before.
gained dominance, regardless of its phase or it being an AI or a real image. The results are therefore consistent with those obtained using AIs alone but suggest that they may not be specific to AIs.

**Rivalry between AIs: Abrupt versus gradual stimulus removal**

In Experiment 4, we tested the hypothesis that it may, in fact, have been the abrupt stimulus change of the sudden removal of the AI-inducing stimuli, rather than monocular adaptation or the nature of the AIs, that may account for the previously suppressed image to become dominant. A mechanism similar to that of flash suppression (Wolfe, 1984), in which dominance is switched to the other eye by the sudden presentation of a new stimulus, may therefore account for the dominance switch between the eyes observed above when the two high-contrast AI-inducing stimuli were abruptly removed.

If the effect observed in the above experiments did have to do with the abrupt stimulus change, we would expect a more smooth removal of the AI-inducing stimuli to reduce the effect: Dominance may then tend to remain in the dominant eye rather than switch to the previously suppressed eye. We therefore repeated Experiment 2 but smoothly faded out the AI-inducing stimuli instead of removing them instantly.

**Methods**

The same procedure and stimuli as described for Experiment 2 were applied, with two differences: There was no strength judgment task, and instead of showing the two AI inducers for 2000 ms (after flash suppression) and then removing them abruptly, both AI inducers were shown for 1750 ms in full contrast (after flash suppression), and then gradually faded out during 500 ms (by linearly reducing contrast over time) to reveal AIs after 2250 ms. The fixation dot then changed to red, indicating to the subject that they now perceived an AI, prompting them to decide and report which AI orientation was perceived. Each of the eight subjects performed 8 blocks of 8 counterbalanced trials. The blocks were counterbalanced to those of the abrupt stimulus removal experiment.

**Results**

Figures 4b and 4c show the outcome when the AI-inducing stimuli were removed abruptly or gradually (Figure 4b is replotted from Figure 2b for comparison, and Figure 4c shows new results of gradual removal). It is apparent that the original finding became inverted when stimuli were gradually faded out, and the probability that the dominant eye remained dominant was significantly higher after gradual fading out of the stimuli compared to abrupt removal of the stimuli ($t(7) = 2.78$, $p = 0.014$).

**Conclusion**

Experiment 4 shows that the dominance reversal in AI rivalry, shown in Experiments 1–3 and by Gilroy and Blake (2005), can be inverted when the AI-inducing stimuli were removed gradually rather than abruptly. This result suggests that the abruptness of the stimulus removal was critical in the previous experiments to render the AI
of the previously suppressed grating dominant. Together with the result of Experiment 3, these findings suggest that the abruptness of the stimulus removal, rather than something AI-specific such as phase inversion, may account for the original finding.

**Rivalry between real images after a brief stimulus interruption**

In Experiment 5 (Figure 5), we tested the hypothesis whether an abrupt stimulus removal may trigger a dominance reversal also during rivalry between real stimuli rather than between AIs.

If the dominance reversal effect observed in above AI Experiments 1–3 did not have to do with AIs, but with the abrupt change in the stimulus when the initial gratings were removed to reveal the AIs, we would expect that the mere presentation of a brief stimulus disruption (with continued full-contrast stimulus presentation following it) would also induce a perceptual switch immediately following the disruption. In fact, dominance reversals due to abrupt stimulus changes have been reported before in various different settings (Bartels & Logothetis, 2010; Blake & Fox, 1974; Blake et al., 1980; Kanai, Moradi, Shimojo, & Verstraten, 2005; Wolfe, 1984). In the following experiment, we thus used similar stimuli as those used in the above AI experiments, but instead of removing them we presented a brief (100 ms) high-contrast interrupting pattern after which the full-contrast rival stimuli were presented again. Apart from the slightly varied stimuli (using gratings of unequal strengths), this experiment is a replication of our prior experiments on this theme (Bartels & Logothetis, 2010). In supplemental experiments, we then repeated this procedure but using short dominance durations, both for real stimuli and for AIs.

**Methods**

Dominance was induced as in the previous experiments using flash suppression (initial grating: 5 cd/m², second grating (dominant): 8 cd/m², 100% contrast, 5 cpd, 0.75-deg width). Instead of removing the physical stimuli after 3 s to reveal AIs, we presented a brief binocular pattern of white noise for 100 ms (8 cd/m², 100% contrast) to mimic the abrupt stimulus change in the AI experiments. After this stimulus interruption, both real stimuli were shown with identical luminance and contrast (6.5 cd/m², 100% contrast). As in the previous experiments, the subjects reported by button press which of the two stimuli they perceived immediately following the interrupting stimuli.

To test whether results were due to eye-based or stimulus-based processes seeking dominance, the two real stimuli were shown either in the same eye as before the interruption or exchanged between the eyes. These trial types were randomly interleaved, and subjects were not aware of this manipulation.

In this experiment, the gratings were tinted light green ($x:0.274, y:0.359$) or magenta ($x:0.255, y:0.255$). The colors were made isoluminant using the minimal flicker method for each subject (Kaiser, 1991) and canceled to gray when combined. Each subject performed at least 5 blocks of each experiment with 16 trials each.

![Figure 5](http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932799/ on 06/09/2018)
Results

In average, the subjects perceived the previously suppressed grating orientation in 79 ± 12.0% (mean ± SD) of trials as dominant after the mask in the same-eye condition (p < 0.0001, n = 7 subjects; all individual subjects reached p < 0.05). When stimuli were exchanged following the mask, again the previously suppressed grating orientation was perceived as dominant, in 65% ± 10.8% of the trials (p < 0.006, n = 7 subjects; 5 out of 7 subjects achieved p < 0.05, one p = 0.06, and one p = 0.60). Therefore, the dominance of the previously suppressed stimulus does not appear to be driven by monococular or eye-based factors but primarily by eye-independent factors, favoring a switch of the percept, regardless of the eye. Note however that eye-based factors also played a role that was minor though, in that the effect was somewhat larger in the same-eye condition compared to the exchanged-eye condition, indicating a small eye-of-origin destabilizing factor (p < 0.013, n = 7 subjects; significant in 4 out 7 subjects with p < 0.05).

We conducted two related supplemental experiments that are reported in Supplementary Figures S1 and S2. In the first supplemental experiment, we repeated the present experiment but using short (300 ms) rather than long (3 s) dominance periods preceding the interruption, in order to replicate our previous finding of a time dependence of rivalry interruption effects (Bartels & Logothetis, 2010). The experimental trials were collected interleaved to those collected for long durations of Experiment 5. The results confirmed that primarily eye-based factors rather than stimulus-based factors determined the outcome after short dominance (in contrast to the above reported findings for long dominance): After short dominance, the dominant grating remained dominant after the disruption in same-eye conditions (p < 0.005, n = 7 subjects), and in the exchanged-eye condition, there was an equal frequency of dominance for both stimuli (see Supplementary Figure S1).

In the second supplemental experiment, we attempted to test whether the same time dependence held true for AI rivalry as well (see Supplementary Figure S2). If this was the case, we would expect less AIs of the suppressed grating to gain initial dominance compared to long dominance trials. We thus replicated Experiment 2 using an AI induction period of 800 ms instead of 2 s. The dominance period could not be reduced to less than 800 ms, as for shorter durations AIs failed to form. It was not feasible to gain contrast judgments as AIs were near threshold of perception after stimulus removal and then rapidly disappeared. Nevertheless, the results were consistent with those obtained for real stimuli: After short dominance, there was no significant tendency anymore of the AI of the previously suppressed stimulus to become dominant. Instead, both previously suppressed and dominant percepts occurred with about equal frequencies (see Supplementary Figure S2). The difference to long dominance trials did not, however, reach significance across the group, probably in part because of the relatively long period required for AI induction.

Conclusion

Experiment 5 shows that a brief stimulus disruption—like that caused by the removal of the AI-inducing stimuli—reliably induced a perceptual switch when subjects viewed real stimuli. Interestingly, this perceptual switch was primarily due to binocular, stimulus-based processes, as it happened regardless of same-eye or exchanged-eye presentation of the stimuli after the disruption. The effect therefore appears to be very robust, as it worked regardless of whether stimuli were shown to the same or to exchanged eyes. It is thus plausible to assume that the same mechanism was at work in the AI experiments, where the sudden removal of high-contrast stimuli would have had a similar effect as the presentation of the interrupting stimulus in this experiment. Additional suggestive evidence comes from the time dependence of this effect, where corresponding AI experiments (shown in Supplementary Figure S2) delivered consistent results.

Discussion

Together, our experiments lead us to make several suggestions. First, our findings suggest that the perceptual switch to the previously suppressed percept—in AI rivalry, the initial dominance of the AI of the previously suppressed stimulus—is brought about by a stimulus disruption and that this is independent of the nature of the stimuli, i.e., AIs or real images. In AI rivalry, this disruption was caused by the sudden removal of high-contrast images, in rivalry between real images by presentation of interrupting pattern. Our Experiment 2 showed that the dominance reversal occurred despite the AI of the previously suppressed stimulus being perceived as weaker in contrast compared to the AI of the previously dominant stimulus. Experiment 3 showed that the phase inversion inherent to AIs compared to their inducers did not alter the outcome, as all AI results were replicated also when weak-contrast real gratings rivaled with one of the AIs, with consistently the previously suppressed orientation gaining dominance regardless of it being an AI or a weak-contrast grating. When, in Experiment 4, the AI-inducing stimuli were phased out gradually instead of removed abruptly, the results reversed, in that the AI of the previously dominant grating tended to remain dominant. This result shows that indeed the abrupt removal caused the dominance reversal in AI rivalry, as it was reduced when the abrupt stimulus removal was avoided. Finally, Experiment 5 showed that also with real gratings an abrupt stimulus interruption induced dominance reversals.
These were so robust that they persisted even when the stimuli were exchanged between the eyes after the interruption. Our supplemental experiments show consistency of AI rivalry with the time dependence observed in real grating experiments, in that the dominance reversal was reduced after short compared to long dominance periods preceding the stimulus interruption.

Together, our results therefore suggest that the dominance reversal observed in AI rivalry is related to the dominance reversal during normal rivalry following abrupt stimulus changes (Bartels & Logothetis, 2010; Kanai et al., 2005; Klink et al., 2008; Noest, van Ee, Nijis, & van Wezel, 2007), which in turn is related to the general phenomenon known as “flash suppression” (Wolfe, 1984). It is a possibility that also changes in the suppressed stimulus that have been reported to lead to a perceptual switch are based on the same mechanism, i.e., that the occurrence of the change itself, rather than the fact that it occurred in the suppressed stimulus, accounts for the switch (Bartels & Logothetis, 2010; Blake & Fox, 1974; Blake et al., 1980; Kanai et al., 2005). Second, the induction of a perceptual switch by a stimulus disruption leaves open two possibilities with regard to its causes. Either the disruption revealed the “urge” of the suppressed monocular or eye-based channel to gain dominance, or it revealed a binocular, perhaps higher level stimulus-related effect favoring a perceptual switch. This question was addressed extensively in our previous study (Bartels & Logothetis, 2010). In it, we demonstrated a time-dependent change in the monocular contribution to stabilize the dominant eye (regardless of the stimulus shown to it) that was strong initially but decreased over time toward zero after a longer dominance period. In addition, there was also a perceptual contribution (regardless of the monocular channel feeding it) that initially stabilized the percept and then decreased over time to destabilize the current percept after a long dominance period. Both eye-based and stimulus-based contributions therefore declined in parallel over time, indicating a dependence of the two (Bartels & Logothetis, 2010). These results were replicated here in Experiment 5 (see also Supplementary Figure S1). Since AI rivalry was induced after long dominance periods (averaging the spontaneous dominance time of 2–3 s), it was primarily the destabilizing perceptual effect that led to the perceptual switch. This is also evident in Figure 5 (Experiment 5 for long dominance): In the same-eye condition, which resembled the AI experiments, both the monocular channel and the percept switched. The exchanged-eye condition disambiguated these two: The percept switched, but the eye-based channel mediating the dominant percept stayed the same. This indicates that the stimulus disruption revealed an “urge” for a perceptual switch that was independent of the eye-based channel.

Our second suggestion is therefore that the stimulus disruption in both AI and real-image experiments led to a perceptual switch originating from a binocular stimulus representation, as it occurred independent of the monocular channel of stimulus presentation. Note though that this effect depends on the preceding dominance time as shown in our previous investigation and in our current replication thereof in Supplementary Figure S1 (Bartels & Logothetis, 2010).

Our final suggestion is a purely hypothetical one and concerns potential neural sources in rivalry.

Negative AIs are believed to be monocular effects, but the perceptual switch induced by a stimulus disruption after prolonged dominance appears to be a binocular effect. Our experiments therefore rule out the suggestion by Gilroy and Blake (2005) that a differential AI strength is causally linked to the perceptual switch. For the same reason, our current and previous experiments also speak against the suggestion that differential adaptation at the monocular level may underlie perceptual switches in rivalry, in that higher as well as lower level mechanisms appear to be involved. Nevertheless, our results are compatible with models of adaptation at several stages (eye-based as well as percept-based) contributing to perceptual switches (Kang & Blake, 2010; Laing & Chow, 2002; Lehky, 1988; Noest et al., 2007; Wilson, 2003) and equally with models based on attractors and noise (Kim, Grabowecky, & Suzuki, 2006; Moreno-Bote, Rinzela, & Rubin, 2007). Since neurophysiology has consistently found either no or extremely weak percept-related spike-rate modulations in monocular channels (in LGN as well as in V1), a direct, e.g., mutually suppressive interaction of eye-based channels, is unlikely to underlie rivalry. The near absent spike-rate modulation in early areas also makes differential spike-rate adaptations due to dominance or suppression an unlikely cause of rivalry. Instead, physiology demonstrated strong percept-modulated spike discharge changes in extrastriate areas (see, e.g., Leopold & Logothetis, 1996) and changes of local field potentials and of fMRI signals in early visual areas (Gail et al., 2004; Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005; Lehky & Maunsell, 1996; Wilke et al., 2006; Wunderlich, Schneider, & Kastner, 2005). The discrepancy between spike-rate modulation, on the one hand, and LFP as well as fMRI signals, on the other hand, in early visual processing may thus be taken to indicate substantial interactions between higher level and early neural processing during rivalry, as both LFP and fMRI signals are strongly affected by synaptic processing such as that induced by feedback signals (Bartels, Logothetis, & Moutoussis, 2008; Maier et al., 2008).

In accord with this, there is psychophysical evidence for a direct interaction between stimulus-based and eye-based processes in rivalry (Bartels & Logothetis, 2010; Ngo, Liu, Tilley, Pettigrew, & Miller, 2007; van Boxtel, Alais, & van Ee, 2008; Watson, Pearson, & Clifford, 2004). For example, two point-like walkers rival when each is presented to a different eye but not when they are presented in an eye-scrambled way (Watson et al., 2004). Similarly, the modulation of AI strength by the
perceptual state indicates feedback to monocular representations (Brascamp et al., 2010; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005).

Therefore, feedback from the dominant binocular stimulus representation may, e.g., reduce noise or affect interneural correlations in the eye-based channels feeding it. This could increase the influence of one of the eye-based channels on binocular levels without affecting spike rates at the eye-based level. In fact, such a high-level effect on eye-based stimulus representations is supported by the finding that attention to AIs reduced their strength, thus enhancing processing of external as opposed to internal (noise) signals (Lou, 2001). Neural noise and interneural correlations have since been shown to play a role in attention, performance, and conscious perception (Cohen & Maunsell, 2009; Mitchell, Sundberg, & Reynolds, 2009; Schurger, Pereira, Treisman, & Cohen, 2010). Therefore, parietal influences on perceptual durations during rivalry may also be based on top-down modulation of noise or interneural correlations in visual areas (Kanai, Bahrami, & Rees, 2010; Zaretskaya, Thielscher, Logothetis, & Bartels, 2010).

This mechanism is also compatible with models of adaptation, may co-determine dominance and suppression during rivalry, and may affect AI formation in the suppressed eye-based or monocular channel. This account appears compatible with differential AI formation, as well as with our current and previous findings on time-dependent eye and stimulus contributions in rivalry (Bartels & Logothetis, 2010; Brascamp et al., 2010; Gilroy & Blake, 2005; Tsuchiya & Koch, 2005).

Conclusion

We investigated the counterintuitive phenomenon of initial dominance of the previously suppressed AI in rivalry and found the reason for it to be a general mechanism, namely, the tendency of the brain toward a perceptual switch after prolonged dominance of one stimulus. While we reproduced the finding that the AI of the previously suppressed stimulus gains initial dominance after the removal of rivaling AI-inducing gratings, we found that this result was not due to the AI’s weakness, it being phase-inverted compared to the real image, or it being an AI as opposed to a real image. Instead, we found the results to be due to a mechanism related to flash suppression that favors a perceptual switch after prolonged dominance. This mechanism appears to originate primarily from binocular stages, and allows a stimulus disruption to trigger the perceptual switch—regardless of the eye-based channel. Furthermore, we speculate that AI formation—that involves mostly early visual eye-based stimulus representations—may be influenced via feedback from binocular, higher level neural stimulus representations onto eye-based and monocular stimulus representations. This influence may affect the strength of AI formation during perceptual suppression in binocular rivalry.

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