Visual suppression at the offset of binocular rivalry

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Various paradigms can make visual stimuli disappear from awareness, but they often involve stimuli that are either relatively weak, competing with other salient inputs, and/or presented for a prolonged period of time. Here we explore a phenomenon that involves controlled perceptual disappearance of a peripheral visual stimulus without these limitations. It occurs when one eye's stimulus is abruptly removed during a binocular rivalry situation. This manipulation renders the remaining stimulus, which is still being presented to the other eye, invisible for up to several seconds. Our results suggest that this perceptual disappearance depends on a visual offset–transient that promotes dominance of the eye in which it occurs regardless of whether the eye is dominant or suppressed at the moment of the transient event. Using computational modeling, we demonstrate that standard rivalry mechanisms of interocular inhibition can indeed be complemented by a hypothesized transient-driven gating mechanism to explain the phenomenon. In essence, such a system suggests that visual awareness is dominated by the eye that receives transients and "sticks with" this eye-based dominance for some time in the absence of further transient events. We refer to this phenomenon as the "disrupted rivalry effect" and suggest that it is a potentially powerful paradigm for the study of cortical suppression mechanisms and the neural correlates of visual awareness.

Introduction

Visual illusions and phenomena have facilitated our understanding of the neuronal mechanisms of visual perception for decades. "Disappearance paradigms" are a popular class of observations, in which visual stimuli that are usually perceived without any difficulty are rendered perceptually invisible for significant durations. Such "invisibility" can be induced at different levels along the vision/attention hierarchy (Breitmeyer, 2015). Phenomena such as inattentional blindness (Mack & Rock, 1998), change blindness (Rensink, 2002), or the attentional blink (Shapiro, Raymond, & Arnell, 1997) are thought to involve high levels of processing whereas binocular rivalry (Blake, 2001; Brascamp, Klink, & Levelt, 2015; Fox, 1991; Levelt, 1965) offers a prominent example in which early visual processing plays an important role. Visible stimuli can either disappear spontaneously (e.g., Troxler fading [Troxler, 1804] or filling in [Walls, 1954]), or they can be rendered invisible through additional competing, interfering, or distracting inputs (Anstis, 2013; Bonneh, Cooperman, & Sagi, 2001; Breitmeyer & Ogmen, 2006; Flom, Heath, & Takahashi, 1963; Kolers & Rosner, 1960; Tong, Meng, & Blake, 2006; Tsuchiya & Koch, 2005; Wilke, Logothetis, & Leopold, 2003).

In most disappearance paradigms, the stimulus that will be rendered invisible needs to be of limited strength, presented for long durations, and/or suppressed by salient competing stimuli. Paradigms in which salient stimuli are suppressed from visual awareness for prolonged periods of time *without* concurrent intra- or interocular competition are rare (Anstis, 2013, Wilke et al., 2003). At the same time, with the advent of neuroimaging tools, exactly such paradigms might be particularly useful in the search for neural correlates of consciousness (Blake, Brascamp, & Heeger, 2014; Cox, Lowe, Blake, & Maier, 2014). After all, if a salient stimulus can be suppressed for seconds on end before spontaneously reappearing and if this suppression does not require any visual transients or sustained competing inputs, its reappearance will constitute a very clean endogenous event specific to the neural mechanisms underlying visual awareness (de Graaf, Hsieh, & Sack, 2012; de Graaf & Sack, 2014).

In binocular rivalry, individual eyes are presented with different, incompatible stimuli, causing visual awareness to continuously switch between the two images with individual dominance durations that depend on stimulus features (Kang & Blake, 2011). In one of our binocular rivalry experiments, we serendipitously observed that abrupt removal of one eye's visual stimulus in a peripheral binocular rivalry display can lead to a surprisingly long-lasting perceptual disappearance of a high-contrast visual stimulus that continues to be presented to the other eye, provided that central fixation is maintained. In what follows, we refer to this phenomenon as the "disrupted rivalry effect" (DRE). Although this phenomenon has previously been alluded to (Leguire & Fox, 1979; Vergeer & van Lier, 2010; Wolfe, 1984), it has to our knowledge not been recognized for its potential value for neuroimaging and perhaps therefore not yet been explored in depth.

We conducted a series of experiments to quantitatively study the DRE phenomenon and performed computational modeling to gain insight into its potential underlying neural mechanisms. Our results suggest that upon abrupt removal of one eye's stimulus during binocular rivalry, visual awareness will (switch to and) "stick with" that eye despite the maintained presence of competing inputs in the other eye. We suggest that the visual offset–transient induced by stimulus removal initially empowers the now unstimulated eye within the context of a reciprocal inhibition mechanism. Subsequently, the visual system may maintain the status quo for some time in the absence of further visual transients. We adapted an existing computational model of visual awareness in binocular rivalry to implement this interpretation and found that a transient-driven gating mechanism could indeed qualitatively explain our empirical findings.

Methods

Participants

For all experiments, participants were volunteers with (corrected to) normal binocular vision who provided written informed consent prior to participation. Experiments were approved by the local ethics committee. Except for experimenters, observers were naïve to the aims of the experiments and generally untrained in performing psychophysics experiments. They were rewarded for participation with monetary coupons. The numbers of participants in each experiment were 12 (Experiment 1, including one experimenter), nine (Experiment 2, including one experimenter), 10 of which one subject was excluded[1] (Experiment 3, including two experimenters), five (Experiment 4, including one experimenter), 10 (Experiment 5), and 10 (Experiment 6).

Stimuli and experimental setup

For Experiments 1 through 3, participants were seated in a fully dark room and viewed two standard TFT monitors (Iiyama ProLite) through a mirror
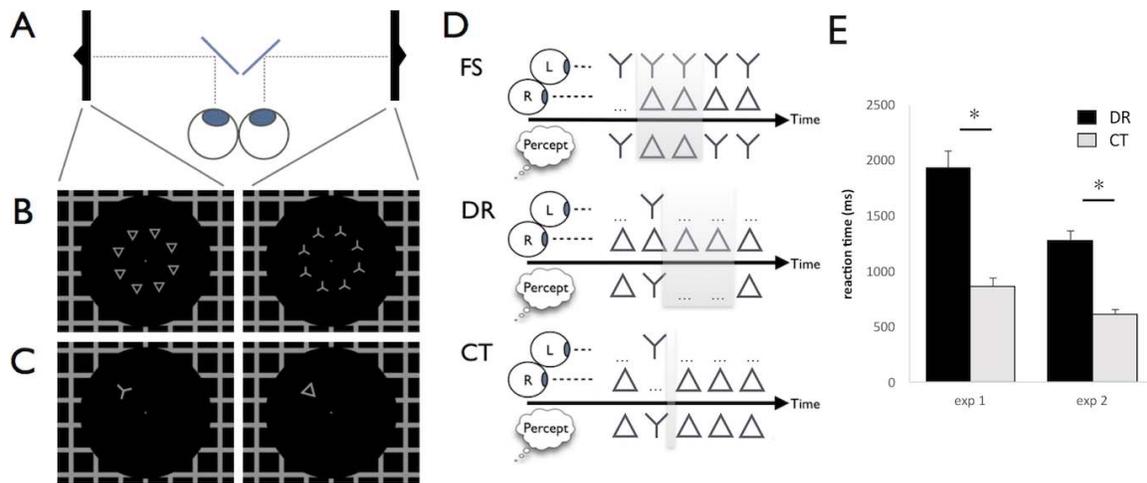
Figure 1. Setup, stimuli, and design. (A) Experimental setup for Experiments 1 through 3: a stereoscope with mirrors and two monitors. (B) Stimuli for Experiment 1. (C) Stimuli for Experiments 2 and 3. (D) Experimental design: FS trials involved adaptation followed by flash suppression and ongoing rivalry. DR trials also involved adaptation and flash suppression but followed by quick removal of the flashed rivalry stimulus, inducing a relatively long suppression of the original, now competition-free, adaptor stimulus. CT trials were trials in which suppression did not occur because the adaptation stimulus was removed during the "rivalry" phase. The shaded gray areas reflect the calculated RTs for different conditions as follows: time from rivalry onset to first subsequent percept switch as indicated by button press (FS), time from rivalry offset to percept return indicated by button press (DR), and "flash offset" to "percept return" indicated by button press (CT). The latter essentially reflects baseline RT. (E) Main results of Experiments 1 and 2, presented separately for the DR and CT conditions. There were significant differences between average median RTs in the DR and CT conditions in both experiments. Error bars reflect standard error of the mean.

stereoscope so that each eye only received input from one of the monitors. This dual-monitor (60-Hz) setup was temporally accurate to one to two frames with the left monitor leading the right monitor. In Experiments 4 through 6, participants were seated in front of a single monitor, and dichoptic stimulation was achieved with either prism goggles and a cardboard separator (Experiment 4; Schurger, 2009) or a conventional mirror stereoscope (Experiments 5 and 6). In all experiments, stimuli were counterbalanced between the eyes across trials. In all experiments, both eyes were presented with a fixation dot and a reference frame in the periphery to guide binocular fusion (Figure 1A through C, Figure 5B). Stimuli differed in the number of elements (eight for Experiment 1, one for Experiments 2 through 4), element position (diagonal to fixation in one of the four visual quadrants for Experiments 2 and 3, always in the upper left quadrant for Experiments 4 through 6), background color (black in Experiments 1 through 3, 5, and 6 but red and green in Experiment 4), and type of stimulus elements. The elements, either Y shapes or triangles, evoked rivalry when spatially superimposed but presented to different eyes (van Ee, 2011). For grayscale stimuli in Experiments 1 through 3, 5, and 6, the stimulus elements, fixation dot, and peripheral frame were presented on black background on Iiyama ProLite monitors in a fully darkened lab with luminance varying across experiments (Experiments 1 through 3: $\sim$9 cd/m^2,

Experiment 5: $\sim$34 cd/m^2, Experiment 6: $\sim$17 cd/m^2). In the eight-element array (Experiment 1), elements were presented at eccentricity 5.7° visual angle (DVA) and comprised 2.7 DVA shape width (diameter of circle spanning the outer points of the Y or triangle shapes) with a line width of 0.33 DVA. For the experiments with single elements, the analogous dimensions were an eccentricity of 6.2 DVA, shape width of 3.5 DVA, and line width of 0.43 DVA for Experiments 2 and 3 and an eccentricity of 5.3 DVA, shape width of 3.3 DVA, and line width of 0.4 DVA for Experiments 4 through 6. Although future studies will explore how the duration of the DRE depends on stimulus parameters, our current results firmly suggest that DRE reliably occurs across a range of parameters and stimulus types. Some preliminary results, however, suggest that although it is difficult or not possible to achieve DRE with foveal presentation, the effect gets more robust with increasing eccentricity. In any case, proper fixation is crucial.

In Experiments 1 through 4, participants were explicitly introduced to the paradigm and the disappearance effect. In demonstration and training runs, it was explained how to fixate, attention was drawn to the disappearance effect, and they were shown what happens when fixation is interrupted by a saccade (i.e., the disappearance effect ends immediately). Experiments 5 and 6 were designed and added explicitly to evaluate DRE in the absence of such instruction.
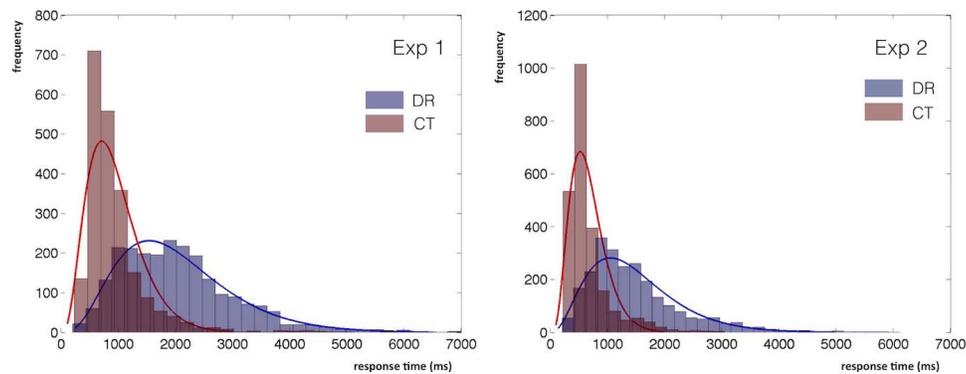
Figure 2. Distributions of RTs. Shown for Experiment 1 (left) and Experiment 2 (right) are distributions (binned histograms) of RTs calculated as indicated in Figure 1D (shaded areas). Graphs present all included trials of all participants, separately for DR condition (blue) and CT condition (red). Gamma distribution fits are superimposed. It is clear that in DR, not only was the mean RT higher; there were also a substantial number of trials in which perceptual disappearance lasted for several seconds. Analogous plots for all individual participants are provided in the Supplementary Material.

Experiment 1: Tasks and design

Experiment 1 developed the "standard" DRE trial structure in the disrupted rivalry (DR) condition. This included three trial phases after a brief fixation period, an adaptation phase, a rivalry phase, and the DRE phase.

In the *adaptation phase* (250, 1000, 1750, 2500, or 3250 ms) an adaptor stimulus (an array of eight peripheral triangle or star elements) was presented to one eye while no competing stimulus elements were presented to the other eye.
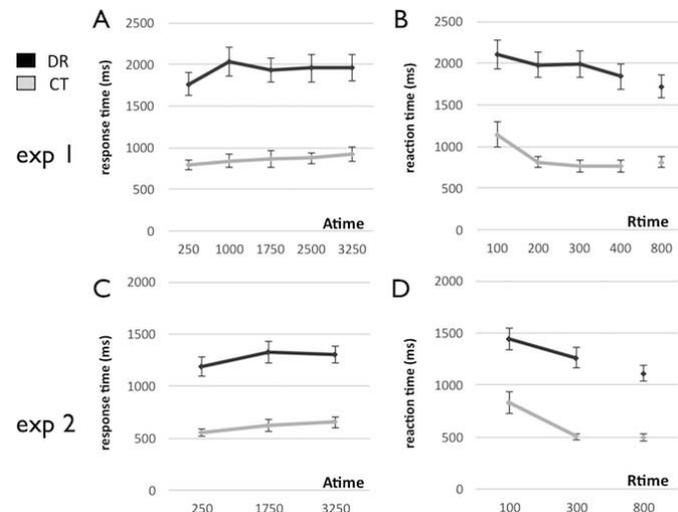

Figure 3. Effects of adaptation and rivalry phase durations (Experiments 1 and 2). (A) Shown separately for DR (dark gray) and CT (light gray) conditions are the RTs (vertical axis) over adaptation phase duration (A-time, horizontal axis). These are the results of Experiment 1. (B) Same as in panel A but shown over rivalry phase duration (R-time, horizontal axis). (C) Same as in panel A but for Experiment 2. (D) Same as in panel B but for Experiment 2. Error bars represent standard error of the mean.

In the *rivalry phase* (100, 200, 300, 400, or 800 ms), the adaptor stimulus remained on the screen but was complemented by a second array of oppositely shaped elements presented to the other eye. This introduction of a second stimulus consistently caused perceptual suppression of the adaptor stimulus—a phenomenon known as flash suppression (Wolfe, 1984).

The *DRE phase* started with the removal of the flashed rivaling stimulus, leaving again only the original adaptor stimulus on the screen. In this phase, participants pressed a button on the keyboard to indicate when, after removal of the flashed stimulus, they perceived the original adaptor stimulus again. This response automatically ended the DRE phase.

The eye to which the adaptor stimulus was shown (left or right) and the type of adaptor stimulus (triangle or Y elements) were counterbalanced and presented in pseudorandom order. In the absence of any disappearance effect, response times (RTs) would denote standard stimulus detection RTs. We controlled for this component of RTs by measuring it directly in a control condition (CT, see below). Because the stimulus consisted of an array of stimulus elements, which are known to evoke inhomogeneous rivalry dynamics (van Ee, 2011), participants were specifically instructed to press the button when *all* stimulus elements were perceived again. Experiment 1 moreover included a secondary task at the end of each trial in which participants used a second button to indicate which stimulus element had been the last to return to conscious perception.

In the CT condition, stimulus events equaled those of the DR condition except that during the rivalry phase the adaptor stimulus elements were removed from the screen. They were displayed again at the offset of the rivalry phase when the flashed stimulus was removed. Due to the reliability of flash suppression in the DR condition, perception in the DR and CT
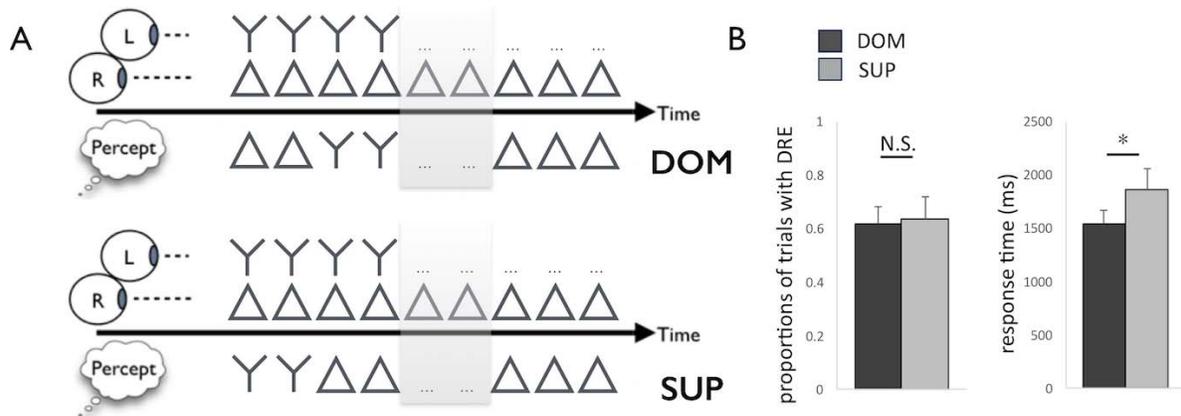
Figure 4. Disrupting ongoing binocular rivalry. (A) Design of Experiment 3. Standard ongoing binocular rivalry was disrupted after a variable period of time by removing one of the two competing stimuli. Participants continuously indicated whether they perceived stars, triangles, or neither of the two. Based on these reported percept sequences, we determined post hoc whether the removed stimulus had been perceptually dominant (DOM) or suppressed (SUP) at the time of removal. Dependent variable for the analysis was the time from rivalry offset to button press indicating percept return (shaded areas). (B) Left: Proportions of included trials in which the suppression effect occurred (see Methods for classification criteria) for conditions DOM and SUP, no significant difference. Right: Average median RTs from rivalry offset for trials in which DRE did occur, separately for DOM and SUP. DRE was significantly longer for SUP trials. Error bars reflect standard error of the mean.

conditions was the same throughout the adaptation phase and the rivalry phase with or without the adaptor stimulus present. However, the removal of the adaptor stimulus during the rivalry phase completely abolished the disappearance effect in the DRE phase, likely due to the additionally evoked visual transients in the eye to which the adaptor stimulus was presented as we discuss later. Finally, a classic flash suppression (FS) condition included the adaptation phase and the rivalry phase, but it lacked a DRE phase as the rivalry stimulus remained on screen until participants reported perceiving all original adaptor stimulus elements again. Two repetitions per design cell (adaptor eye × adaptor stimulus × FS/DR/CT × adaptation duration × rivalry
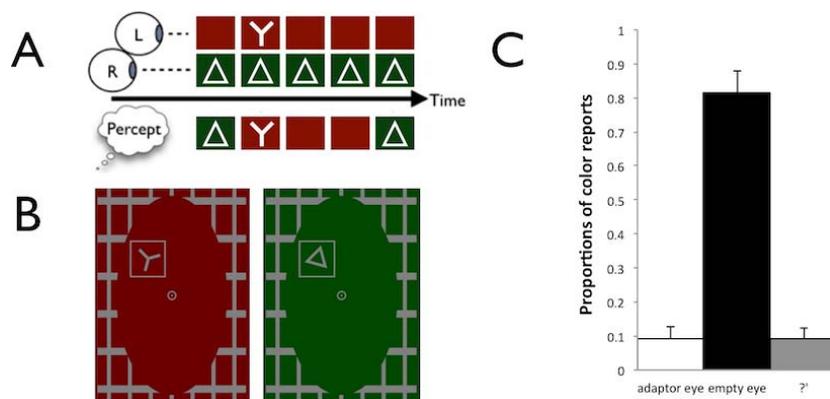

Figure 5. Which eye is represented during DRE? (A) Schematic depiction of the design and crucial result of the experiment; in this example, the right eye was the "adaptor eye." Both eyes received differently colored backgrounds (red or green) on top of which single stimulus elements were presented. Participants performed the standard DR task, indicating percept return. But immediately afterward, they also indicated whether they had perceived a red or green background inside the square outline during the suppression period unless they could not confidently perceive or remember (response option "?"). (B) The actual stimuli. Colors, stimuli, and adaptor eye were all balanced. (C) Results, showing the mean proportions of the three different response options. For the example trial in panel A, "adaptor eye" would mean that participants reported seeing green inside the square outline during the suppression period after the rivalry flash, "empty eye" means they reported seeing red, and "?" means they could not remember or did not clearly perceive the color. Results clearly suggest that the perceived color was generally the background presented to the empty, "flashed," rivalry eye in the example trial that would have been red. Error bars reflect standard error of the mean.

duration) resulted in 440 trials per participant, acquired over two runs.

Experiment 2: Tasks and design

Experiment 2 replicated Experiment 1 with a few modifications. Instead of eight stimulus elements, only a single stimulus element was presented in one of the four visual quadrants in each trial. This allowed participants to fully focus on this single element, ruling out any effects of attention, serial search, or lower or higher level interelement competition as a driving mechanism behind the effects shown in Experiment 1. Only three adaptation phase durations (250, 1750, and 3250 ms) and rivalry phase durations (100, 300, and 800 ms) were implemented in this version of the experiment to accommodate the higher number of trials required for the four stimulus element positions. Two repetitions per design cell (adaptor eye × adaptor stimulus × FS/DR/CT × element position × adaptation duration × rivalry duration) resulted in 672 trials per participant, acquired over two runs.

Experiment 3: Tasks and design

In Experiment 3, we focused on the DR condition, which was adapted to disrupt ongoing binocular rivalry rather than relying on flash suppression as we did in the previous experiments. Thus, there was no quick succession of onset and offset transients in the flashed eye and only a relatively unpredictable offset transient during ongoing rivalry in either the dominant or suppressed eye. The single-element stimuli from Experiment 2 were presented simultaneously to the two eyes in one of the four visual quadrants (randomly assigned). One stimulus was then removed at a pseudorandom moment between 4000 and 9000 ms after onset (steps of 1000 ms), and the remaining stimulus remained on the screen for another 4000 ms until the end of the trial. Participants used a computer mouse to continuously indicate whether they perceived a triangle (left mouse button) or star (right mouse button) element by pressing and holding the corresponding mouse button. Whenever neither stimulus was perceived (as is the case during DRE) participants released both mouse buttons.

These responses were used to assign experimental condition labels to trials post hoc. Trials were labeled dominant (DOM) when the removed stimulus was perceived at the time of removal and labeled suppressed (SUP) when it was not perceived at that time. In total, 192 trials were collected per participant in four runs, of which the post hoc labeling was approximately evenly distributed between DOM (842) and SUP (886).

Experiment 4: Tasks and design

In Experiment 4, the stimulus backgrounds were not black, and each eye had its own individually colored background for the complete duration of the trial (red or green). Because we now used the single monitor with prism glasses setup, for this and subsequent experiments stimulus fixation dots and fusion-guiding peripheral frames were slightly adapted as shown in Figure 5B. Trials had a standard DR structure with a fixed adaptation time of 1750 ms and a fixed rivalry time of 300 ms.

Aside from the standard task of indicating the return to perception of the adaptor stimulus in the DRE phase, there was a secondary task at the end of each trial. Throughout a trial, stimulus elements were presented inside a gray square box outline in the upper left quadrant. At the end of each trial (96 in total), participants were asked which color they had perceived within this outline during the DRE phase (i.e., from rivalry offset until perceived reappearance of the adaptor stimulus). With a key press, observers indicated whether that color had been (a) red, (b) green, or (c) not remembered or not perceived clearly enough to make that judgment. For analysis, these responses were recoded to indicate perception of the background presented to the adaptor stimulus' eye or the background presented to the other eye.

Experiments 5 and 6: Tasks and design

The aim of our final control experiments was to replicate the main finding that DRE exists with a duration of up to a few seconds under different attentional conditions. Participants had not taken part in the earlier experiments, and we changed the instructions such that they were completely naïve to the disrupted rivalry disappearance effect. Moreover, the trial structure in our control condition was changed. The new control condition (CT2) presented sequentially the adaptor stimulus, the flashed rivaling stimulus, a (new) period of "no stimulus" of which the duration was dependent on individual participants' DRE durations reported in recent trials, and finally a ramped physical stimulus return to which participants responded by key press. This CT2 condition thus more closely mimics the perceptual sequence of standard DR trials, possibly resulting in more reliable estimates of reaction time to stimulus return. Last, we included a secondary response screen, allowing participants to indicate whether or not the adaptor stimulus had disappeared at all after the flashed rivalry stimulus. Experiment 6 was a replication of Experiment 5 with several small methodological adaptations. More de-

tailed explanations, methods, and all results are presented in Supplementary Material.

Analyses

The main dependent variable across experiments was the time from rivalry phase offset to a button press indicating the return to perception of the adaptor stimulus. Depending on experimental condition, this measure reflects the combined disappearance effect and baseline RT (in the DR condition), the baseline RT alone (in CT), or the postflash suppression dominance time (in FS).

In Experiment 3, as in the other experiments, DRE duration was defined as the moment of indicated percept return, time-locked to the removal of one rivaling stimulus. A valid trial with DRE involved the release of both buttons (indicating "no percept") followed by a button press corresponding to the remaining stimulus element (indicating onset of percept). If buttons were released after the disruption of rivalry but no key press followed within the 4000-ms period that remained in the trial, RT was fixed to 4000 ms. This occurred in ~5% of all included trials with a disappearance effect. This, and other analyses of DRE durations in Experiment 3, were performed only on trials in which DRE unambiguously occurred. Thus, we determined *first* in which trials DRE occurred at all. Note that on DOM trials without a disappearance effect, participants should have indicated an instantaneous percept switch (from the previously dominant but now removed stimulus to the one remaining and immediately perceived stimulus). However, due to practical constraints, the corresponding act of "instantaneously" releasing one and pressing the other mouse button led to brief periods of errantly recorded "no percepts" whenever the release preceded the press. We circumvented this issue by conservatively labeling trials as having induced a DRE only if a stimulus offset was reported within 1500 ms of binocular rivalry offset, followed minimally 300 ms later by a reported stimulus onset of the correct stimulus type or trial end. Note that although this procedure successfully flags trials in which DRE was unequivocally induced, the trade-off is a potential underestimation of DRE proportions and a potential overestimation of median DRE durations.

Preprocessing of data for Experiments 1 through 3 involved the removal of "failed" or outlier trials. Failed trials were trials in which the required button presses were not delivered at appropriate times (e.g., prior to or during the rivalry phase) or in an inappropriate order. In Experiments 1, 2, 5, and 6, we also excluded trials with extreme value RTs. Extreme values were defined as RTs that were below 200 ms or minimally three times the interquartile range above the median,

determined separately per subject and condition (FS, DR, CT/CT2). In Experiment 3, because we needed to post hoc label trials as DOM or SUP based on the temporal pattern of reported perception, we conservatively excluded trials in which we could not be sure of the percept sequence before and after stimulus removal, which was the case if perceptual events (perceived stimulus onset or offset) were reported right around the moment of rivalry offset. Concretely, trials were excluded if a perceptual event (stimulus onset or offset) was reported within 200 ms of rivalry offset (before or after). After preprocessing, the percentages of included trials (mean and standard error of the mean, in parentheses, across participants) were 93.7% (2.3%) in Experiment 1, 94.4% (5.3%) in Experiment 2, 79.8% (2.3%) in Experiment 3, 98.7% (0.0%) in Experiment 5, and 98.5% (0.0%) in Experiment 6.

The estimator of RTs used in all experiments was the median RT (because RTs were not normally distributed; see Results), determined separately per participant and condition. In analyses in which RTs were collapsed across conditions (see Results), this involved calculation of the average of individual medians in collapsed conditions. Repeated-measures (RM) ANOVAs were performed on the medians with additional follow-up RM-ANOVAs and follow-up paired-samples t tests as indicated in the Results section. In case of violation of the sphericity assumption (Mauchly's test), Greenhouse-Geisser corrected results are presented. Statistical analyses were done using SPSS software (IBM, Armonk, NY). In Experiment 3, in a post hoc analysis, we correlated standardized percept durations prior to rivalry offset (dominance and suppression times, depending on DOM or SUP conditions) with standardized DRE durations after rivalry offset. We standardized separately the percept durations and DRE durations for which we used participant- and condition- (DOM/SUP)-specific mean RTs and standard deviations to transform all values to z scores by (value − mean)/standard deviation. Only trials with DRE and durations not lasting until end of trial (i.e., 4000 ms) were included. Pearson correlations were calculated for all trials of all participants together but separately for DOM and SUP.

Error bars in figures always reflect standard error of the mean over observers.

Computational modeling

Given that the methodology behind and development of the computational model was inextricably linked to the performance of the model, corresponding methods and analyses are included in the Results section and detailed in the Supplementary Material.

Results

We first present our series of behavioral experiments, followed by the computational modeling steps and results. Of the latter, several logical iterations of the model are detailed in the Supplementary Material, and the final model is presented in the main text in more detail.

DRE: Behavioral results

Experiment 1: DRE and stimulation parameters

In Experiment 1, an array of eight adaptor stimulus elements (see Figure 1B) was presented to one eye for durations ranging from 250 to 3250 ms (A-time). We refer to these stimuli as the "adaptor stimulus" and this phase as the "adaptation phase." A competing array ("rivalry stimulus") was then briefly presented to the other eye for several hundreds of milliseconds (100 to 800 ms, R-time). We refer to this as the "rivalry phase." Upon removal of this flashed rivalry stimulus, participants generally did not immediately perceive the remaining adaptor stimulus even though it was now free from competition with other stimuli. We dubbed this postrivalry period of adaptor stimulus suppression the "DRE phase."

Participants used button presses to report when all stimulus elements in the adaptor array had become fully visible again after being suppressed by the flashed rivalry stimulus (DR condition). This took on average (average of individual medians) 1927 ms ($SEM = 152$ ms). Unsurprisingly, this was shorter than with regular flash suppression (FS condition), with which the flashed stimulus was not removed and adaptor stimuli fully returned to perception after 5506 ms ($SEM = 832$ ms). More importantly, in the CT condition, when the presentation of the adaptor stimulus was temporarily discontinued during presentation of the flashed rivalry stimulus, RTs were much shorter (861 ms, $SEM = 78$ ms). Our own observations, confirmed across replications, suggested that DRE does not occur in this condition. Instead observers immediately perceive the adaptor stimulus upon removal of the flashed stimulus. RTs should therefore reflect baseline reaction speed for the current stimuli and task. In Experiment 1, these responses were a bit slow perhaps because participants checked whether all eight elements were truly visible before they responded. Average medians for these conditions are shown in Figure 1E, and Figure 2 depicts the distributions of RTs over all observers for the DR and CT conditions, showing that although the average median duration of the effect may have been around 2 s, RTs in many trials were quite a bit longer than that. These distributions are also presented for all individual participants in the Supplementary Material.

To explore the effects of stimulus presentation parameters (A-time, R-time) on the duration of the DRE, we performed two RM-ANOVAs. A RM-ANOVA with factors Condition (FS, DR, CT) and A-time (five levels) investigated the effect of adaptation phase duration, and a RM-ANOVA with factors Condition (DR, CT), A-time (five levels), and R-time (five levels) looked into the effect of the rivalry phase duration (see Methods for details). In the Condition × A-time RM-ANOVA, there was a strong main effect of Condition, $F(1.0, 11.4) = 25.9$, $p < 0.001$, but no effects of A-time and no interaction ($ps > 0.1$). Follow-up pairwise comparisons for Condition were all significant (all $ps < 0.01$, Bonferroni corrected).

We next analyzed Condition (DR, CT) × A-time × R-time. There were no significant three-way or other interactions involving factor A-time ($ps > 0.1$). In this analysis, A-time did show a main effect, $F(4, 44) = 7.3$, $p < 0.001$. There were also main effects of Condition, $F(1, 11) = 68.5$, $p < 0.001$, and R-time, $F(1.6, 17.4) = 15.1$, $p < 0.001$, but, moreover, a Condition × R-time interaction, $F(4, 44) = 4.7$; $p = 0.003$. Therefore, we show results separately for the DR and CT conditions in Figure 3. Analyzing R-time separately for DR and CT in RM-ANOVAs (collapsing over levels of A-time) resulted in effects of R-time in both conditions: DR, $F(4, 44) = 14.6$, $p < 0.001$; CT, $F(1.3, 13.7) = 8.8$, $p = 0.008$, but with different origins as is clear from Figure 3. It appears that R-time has a linear inverse effect on RT in DR—polynomial linear contrast on equidistant levels 1:4 of factor R-time, $F(1, 11) = 36.4$, $p < 0.001$—and the effect in CT is driven by a peak in RT for the shortest R-time duration. This may be a surprise effect because with this shortest rivalry duration, motor preparation time was limited (for CT, polynomial contrasts support a linear but also a quadratic data pattern, reflecting this observation).

The secondary task in Experiment 1 was to indicate at the end of each trial which stimulus element in the array had been the last to return to awareness. Previous research demonstrated that competition in binocular rivalry is local and dominance durations spatially inhomogeneous (Carter & Cavanagh, 2007; van Ee, 2011). We analyzed response distributions over the eight stimulus element locations in the stimulus arrays with chi-square tests and refer to the Supplementary Material for full analyses and results, which suggest that idiosyncratic spatial biases are present in the DRE as well.

Experiment 2: DRE for a single stimulus element

Although the task in Experiment 1 was definitely feasible, the use of a circular array of stimulus elements did raise some methodological issues. It made the task of reporting dominance more difficult because compe-

tition and recovery from suppression were local and percept changes therefore inhomogeneous across the array. Participants needed to divide spatial attention across the visual field and keep track of perceptual changes in eight locations simultaneously. Moreover, we could not exclude that the mere presence of multiple stimuli might have led to (competitive) interactions between the representations of these stimuli. To address these issues, in Experiment 2, we studied whether DRE also occurs when there is only one stimulus element. Participants know where the stimulus is, the location is fully attended, and the stimulus cannot differentially interact on any level with other stimulus elements on screen. The results show that, even in isolation and under fully focused attention, stimulus elements were suppressed for prolonged durations.

As shown in Figures 1E and 2, the results largely mirrored those from Experiment 1 although RTs in all conditions were a little shorter (FS: 2647 ms, *SEM* = 142 ms; DR: 1270 ms, *SEM* = 89 ms; CT: 613 ms, *SEM* = 46 ms). In the RM-ANOVA with factors Condition (FS, DR, CT) × A-time (adaptation duration: three levels), there were main effects of Condition, $F(1.2, 9.9) = 141.6$, $p < 0.001$, and A-time, $F(1.1, 8.9) = 9.2$, $p = 0.013$, but no interaction ($p > 0.1$). The RM-ANOVA with factors Condition (DR, CT) × A-time (three levels) × R-time (rivalry duration: three levels) revealed main effects of Condition, $F(1, 8) = 122.5$, $p < 0.001$; A-time, $F(2, 16) = 9.9$, $p = 0.002$; and R-time, $F(1.1, 8.8) = 22.0$, $p = 0.001$, and a trend for an A-time × R-time interaction, $F(4, 32) = 2.2$, $p = 0.09$. Because the latter did not reach significance, no further tests were performed although Figure 3 includes specific results from Experiment 2 to facilitate visual comparison with Experiment 1 results.

On the whole, as seen in Figure 3, the patterns of effects over A-time and R-time were quite similar between Experiments 1 and 2. These experiments provide some support for an effect of adaptation time on RT in the DR condition, yet this support is limited by the fact that similar effects were obtained for the CT condition. Future studies should aim to clarify and confirm the role of adaptation duration on DRE duration. An inverse relationship between rivalry duration (R-time) and suppression duration as measured by RTs is more strongly supported by our current data.

Experiment 3: Disrupting ongoing binocular rivalry

In Experiment 3, we evaluated whether DRE occurred with removal of either the dominant or suppressed stimulus after, on average, 6.5 s of ongoing binocular rivalry. Note that in previous experiments the removed stimulus was always dominant, and in the current implementation, only an offset transient was

presented to one eye (see Methods and Figure 4A). Because participants continuously reported whether they perceived a Y, a triangle, or nothing at all, we could post hoc label trials as DOM or SUP (trials in which this was uncertain were excluded, see Methods).

DRE still unambiguously occurred in approximately 63% of trials included in the analysis (see Methods) as shown in Figure 4B. Interestingly, the likelihood of the disappearance effect occurring did not depend on whether the offset–transient happened in the dominant or suppressed eye: mean proportions, with standard error of the mean in parentheses, of trials with a DRE: DOM 0.62 (0.06), SUP 0.64 (0.08), $t(8) = -0.4$; $p > 0.1$. However, the duration of DRE was slightly but significantly longer in SUP trials (1863 ms, $SEM = 196$ ms) than in DOM trials (1536 ms, $SEM = 131$ ms), $t(8) = -2.8$, $p = 0.024$, two-sided (see Figure 4B, RT distributions provided in Supplementary Material). Apparently, an offset–transient in either eye can be enough to evoke enduring perceptual dominance of this eye without it receiving any further inputs and while supposedly receiving inhibition from the sustained competing inputs in the other eye.

If DRE is (partly) a binocular rivalry phenomenon, we should expect adaptation mechanisms to play a role. Because most reciprocal inhibition models of binocular rivalry comprise dominant channels that weaken over time while suppressed channels gradually regain strength (Alais, Cass, O'Shea, & Blake, 2010), we might find opposite correlations for SUP versus DOM trials between the dominance duration of the percept just prior to rivalry offset (i.e., stimulus removal) and the duration of DRE immediately after rivalry offset. In a post hoc Pearson correlation analysis on *z* scored (see Methods) percept durations prior to rivalry offset and DRE durations postrivalry offset, including trials from all subjects with DRE occurrence but not if it lasted until the end of a trial and separately for DOM and SUP, we did observe this pattern. For DOM trials, there was a significant negative correlation, $r = -0.187$, $p < 0.001$, and for SUP trials, a just significant positive correlation, $r = 0.098$, $p = 0.049$. Note, however, that these effect sizes are quite weak despite the large numbers of included data points. We therefore conclude that the influence of adaptation mechanisms again receives weak support from our data.

Experiment 4: Eye dominance during DRE

The perceptual invisibility of the one remaining stimulus in DRE could, a priori, have two categorically distinct causes. Either awareness reflects the contents of the unstimulated eye (i.e., no stimulus), or awareness reflects the contents of the stimulated eye, but the stimulus in that eye is rendered invisible by processes not directly related to interocular suppression (e.g.,

mechanisms of fading/filling-in). In Experiment 4, we aimed to address this central question: Which eye dominates visual awareness during DRE?

Both eyes were presented with their own constant, but differently colored, backgrounds throughout each trial. Participants were asked to indicate after each DR trial which background color they had perceived at the stimulus element location *during the DRE period* when the element itself was rendered invisible. We coded and present the results as dominance for the "adaptor eye" when the reported color matched the color presented as background to the continuously presented adaptor stimulus or as dominance for the "empty eye" when the reported background color matched the one in the flashed "rivalry eye." Note that during the DRE phase, this empty eye was not presented with a stimulus element. In spite of potential difficulties posed by large-field color rivalry occurring simultaneously throughout DRE trials, participants on the whole considered the task feasible. Participants reported in 9.2% of all trials that the background color had either been unclear or not remembered and in 9.2% of trials that the background color that was presented to the stimulated (adaptor) eye had been perceived during DRE. In the overwhelming majority of trials (81.6%), awareness during DRE reflected the contents of the unstimulated eye (the "flashed," "rivalry," or "empty" eye; $p < 0.01$). Based on our own observations, we suspect that the rare adaptor eye reports reflect errors in reporting or memory rather than exceptional perceptual events with alternative underlying mechanisms.

Experiments 5 and 6: Effects of anticipation, instructions, and control condition

In Experiments 1 through 4, participants were explicitly instructed about the DRE. They were told a priori that the effect exists, were briefly habituated to experiencing it, and they were shown what happens with loss of fixation. Such extensive instructions could have facilitated an attentional process that may be crucial for DRE to occur. Moreover, the perceptual sequence in trials of the CT condition did not resemble DR trials very well. These factors were addressed in Experiments 5 and 6 with an improved CT2 condition and written instructions to naïve participants that only emphasized proper fixation and a quick button press as soon as the adaptor stimulus was again fully and clearly visible (see Methods and Supplementary Material for further details). As reported in the Supplementary Material, DRE was replicated, and effect durations were of the same order of magnitude as previously observed. Data also suggested that DRE did not occur in all trials, which could indicate that

attentional mechanisms may influence the effect, yet it is unclear to what extent this is attributable to lack of fixation or response criteria, and several caveats are in order (detailed discussion in the Supplementary Material).

DRE: Computational modeling

To explore the possible mechanisms underlying DRE, we adapted a frequently used computational model of visual rivalry (Noest, van Ee, Nijs, & van Wezel, 2007). Although this model has proved capable of explaining a multitude of binocular rivalry effects (Brascamp et al., 2008; Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Brascamp, Pearson, Blake, & van den Berg, 2009; Klink, Noest, Holten, van den Berg, & van Wezel, 2009; Klink et al., 2008; van Ee, 2009), its simplest form, containing only adaptation and reciprocal inhibition, could not reproduce the perceptual effects of DRE. We therefore implemented two additional, biologically plausible, functional components, namely (a) a critical role for visual transients and (b) a mechanism to temporarily stabilize visual percepts once they are established.

With these elements, our model could reliably replicate our current DRE findings as well as simulate conventional binocular rivalry and flash suppression. Based on the proposed functional components, we tested several scenarios in which the hypothesized influence of transient stimulus events could potentially result in the observed pattern of behavioral data and found that only one of four model implementations was compatible with the complete set of behavioral results. The basic binocular rivalry features and key findings of the current study that we required our model to reproduce, were the following:

A. Basic features
   1. Produce perceptual alternations in a standard binocular rivalry setting
   2. Reproduce flash suppression—if one eye is stimulated prior to the onset of the stimulus in the second eye, the second eye's stimulus immediately becomes dominant after onset (FS condition)
B. Specific DRE features
   1. Removing the flashed and now dominant stimulus in a flash suppression paradigm results in the DRE, i.e., a substantial period during which the one remaining stimulus is not perceived (DR condition)
   2. If, in a flash suppression paradigm, the initially presented adaptor stimulus is removed from the screen during the presentation of the flashed stimulus, DRE does not occur (CT condition)
   3. If one of the stimuli is removed from the screen during a continuous rivalry display, the remaining

stimulus does not immediately become dominant. Observers instead perceive no stimulus at all for several seconds. This happens regardless of whether the removed stimulus is dominant or suppressed at the moment of removal (Experiment 3).

A minimal binocular rivalry model

The used binocular rivalry model (Noest et al., 2007) is a minimalistic model, the dynamics of which can be described by only two differential equations (Equations 1 and 2).[2]

$$\tau \partial_t h_i = X_i - (1 + A_i)h_i - \gamma S[h_j] \quad (1)$$

$$\partial_t A_i = -A_i + \alpha S[h_i]; \qquad i, j \in \{1, 2\}, i \neq j \quad (2)$$

These equations describe the dynamics of the "field" activity of a population of neurons H on a fast timescale τ (converted into a simulated spike rate by sigmoid function S). The neurons are driven by stimulus input X, and their activity levels depend on adaptation A and cross-inhibition γ from a competing population of neurons. The adaptation dynamics described in Equation 2 have the form of a straight-forward leaky integrator acting on slower timescale t. A simplified wiring scheme of the model is shown in Supplementary Figure S10, in which *E1* and *E2* denote input to individual eyes and *S1* and *S2* are competing populations of neurons. This simple model accurately reproduces both regular binocular rivalry behavior and flash suppression (features A1 and 2), but it fails to demonstrate the DRE (B1 through 3). Instead it immediately switches dominance to the remaining stimulus when one eye's stimulus is removed.[3]

Additive transient-selective neurons

DRE could be qualitatively simulated if stimulus onsets and offsets were treated as additive input signals for eye-selective populations of transient detection neurons. The simplest implementation of transient selectivity in the current model would be an additive contribution of neurons that selectively respond to transient changes in stimulus strength. To this end, we added two pools of such transient-driven neurons to the model, one for each eye (*T1* and *T2* in the wiring scheme of Supplementary Figure S11). Their dynamics follow Equations 1 and 2 with the only difference that they are driven by changes in stimulus strength rather than by stimulus strength itself (Equation 3).

$$XT_i = |\delta X_i / \delta t| \quad (3)$$

The output of these eye-based, transient-selective neurons was added to the output of the sustained activity neurons (*S1* and *S2*). This model satisfied criteria A1, A2, and B1 (DRE in the DR condition) and B2 (no DRE in the CT condition). However, this model only reproduced very short-lasting DREs (on the order of 100 ms) rather than the observed disappearance periods that could last for seconds. Moreover, the results of Experiment 3 (B3) were not reproduced. See Supplementary Material for further information.

Transient-induced interocular gain control

The next scenario we explored was a differential transient-induced interocular gain control mechanism by which the detection of a transient event in one eye would result in an attenuation of the input to the sustained neurons coding for the opposite eye (see circuit in Supplementary Figure S13). We made this a differential mechanism that takes the occurrence of transient events in both eyes into account. It calculates a transient contrast (TC) between the activity of the transient neurons of the two eyes by dividing their difference in activity by their mean (Equation 4). This yields TC values between zero (no difference) and two (maximum difference). If the TC crosses a predetermined threshold (0.75 in our simulations), the input gain for the eye with the lowest activity in the pool of transient neurons is reduced by an amount that depends on the magnitude of TC (Equation 5) for as long as these conditions are met. In the absence of a significant TC, the eye prominence signal and corresponding input gain slowly, but exponentially, return to their original value (Equation 6).

$$TC = \frac{T2 - T1}{(T1 + T2)/2} \quad (4)$$

$$\delta g_i / \delta t = -0.1 TC \quad (5)$$

$$\delta g_i / \delta t = 0.02 g_i \quad (6)$$

This model satisfied A1 and 2, B1 and 2, and now B3 as well. However, the model was limited in several regards and incompatible with our results from Experiment 4 as is discussed in the Supplementary Material in more detail.

Transient-induced ocular gating

When we subjected the output of the rivalry model to a transient-driven gating mechanism, all the behavioral findings could be successfully reproduced. This last model again uses the TC between the eyes to modulate the dynamics of the network. Instead of modulating the input efficacy as in the transient-evoked interocular gain control model, it now acts as a gating mechanism on the output of the rivalry process. If the TC crosses the predefined threshold (again 0.75), this

gating mechanism uses a winner-take-all rule to preferentially allow information of the eye channel with the highest transient-evoked activity to be further processed by other brain areas (e.g., areas higher up the visual cortical hierarchy) while the information of the other eye channel is blocked from further processing by setting its output gain to zero (Figure 6E). In the absence of a significant TC, the gating mechanism lets both signals pass through, and the model is essentially identical to the minimal binocular rivalry model we started off with.

Simulations with the transient-induced gating model reproduced all features (A1 and 2, B1 through 3) of the data (Figure 6). Normal continuous rivalry dynamics and flash suppression were observed (Figure 6A). Removal of a flashed stimulus resulted in a prolonged dominance of the nonstimulated eye (DRE) rather than perception of the remaining stimulus—an effect that was absent when the adaptor stimulus was removed from the screen during flash presentation (Figure 6B, C). Furthermore, the duration of prolonged dominance was on the order of magnitude we expected from the behavioral data (Experiments 1 and 2). Finally, removal of one of the stimuli during continuous binocular rivalry resulted in a period of dominance for the now nonstimulated eye (Experiment 3) regardless of whether the removed stimulus was dominant or suppressed at the time of removal (Figure 6D). The gating mechanism explicitly predicts that, in the period after stimulus removal, the lack of perception of the remaining stimulus is due to dominance of the unstimulated eye and not caused by perceptual fading of the remaining stimulus (a prediction that originally inspired Experiment 4).

Discussion

The current series of experiments explored a phenomenon we refer to as the DRE. Although some previous studies made use of this phenomenon (Leguire & Fox, 1979; van Lier & de Weert, 2003; Vergeer & van Lier, 2010), an extensive exploration of its underlying mechanisms has, to our knowledge, not been performed. Yet DRE not only reflects an interesting and surprising visual effect, it may also have powerful applications as a neuroimaging paradigm for studies of visual processing and visual awareness (de Graaf et al., 2012; de Graaf & Sack, 2014). Below, we first summarize the findings from our experimental investigation of the DRE phenomenon. We then relate DRE to previously reported visual phenomena and mechanisms and outline how DRE may be of methodological value.

Overview of behavioral results

In Experiments 1 and 2, we developed a controlled DRE paradigm. One eye is continuously presented with a monocular stimulus (adaptor stimulus). After a rivaling stimulus is briefly flashed to the other eye, participants can report perceiving no stimulus at all for durations ranging from hundreds of milliseconds to several seconds. We explain this prolonged suppression of the adaptor stimulus through a strong inhibitory drive from the abrupt visual onset/offset transients in the flashed rivalry eye coupled with subsequent percept maintenance through a transient-induced gating mechanism. If transients are presented to the adaptor eye, DRE does not occur (CT condition). Binocular rivalry mechanisms, such as reciprocal inhibition and adaptation, would predict longer-lasting DREs for longer preflash adaptation (A-time) and shorter flash durations (R-time). This predicted effect for rivalry duration was statistically supported; the predicted effect of adaptation duration less so. Experiment 3 demonstrated that the initial flash suppression is not necessarily required to induce DRE: In a majority of ongoing binocular rivalry trials, DRE was also observed upon rivalry offset, irrespective of whether the removed stimulus had been dominant or suppressed. In Experiment 4, we used colored backgrounds to show that, during DRE, visual awareness locally represents the eye that is not presented with a stimulus element (i.e., the recently flashed eye). In Experiments 5 and 6, we replicated the main findings using different parameters, improved control conditions, and fully naïve participants.

The mechanisms underlying DRE: More than binocular rivalry?

At first glance, the main candidate to explain perceptual disappearance during DRE involves binocular rivalry suppression mechanisms. Although it seems unusual that one eye's salient and sustained visual input could be suppressed by the other eye while it no longer receives any driving input in the corresponding spatial location, it has previously been reported that even with one eye patched, a weak form of binocular rivalry persists and influences visual awareness (González, Weinstock, & Steinbach, 2007). A binocular rivalry interpretation of DRE is supported by effects of adaptation time (weak evidence) and rivalry time on DRE duration (Experiments 1 and 2), DRE duration being spatially heterogeneous (Experiment 1, see also van Ee, 2011), correlations of standardized durations of percept dominance or suppression prior to rivalry offset with standardized durations of DRE (Experiment 3, small effect sizes), and the finding that
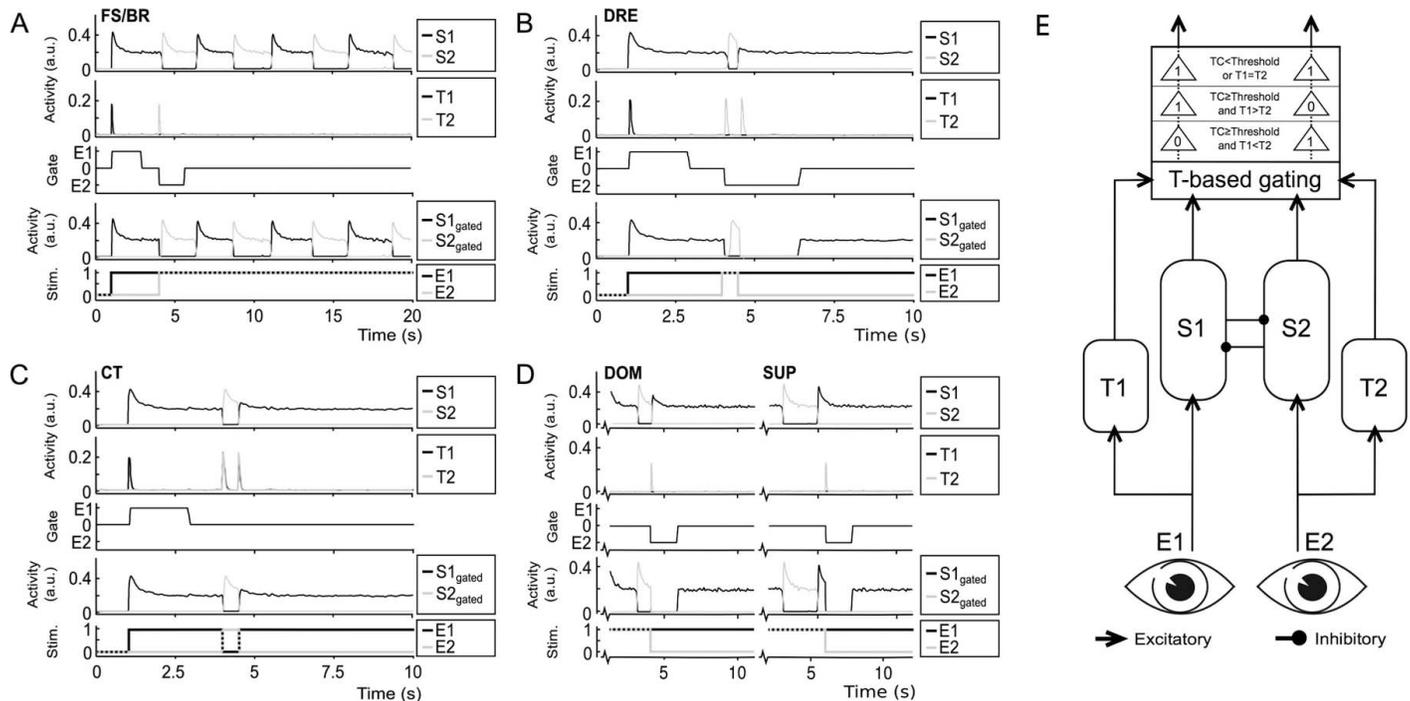
Figure 6. Computational modeling of DRE. (A–D) Rows depict the stimulus drive for either eye (E1 and E2), the response of the corresponding sustained and transient-selective neurons (S1, S2 and T1, T2, respectively), the selection signal of the gating mechanism, and the gated output signal of the sustained populations (S1gated and S2gated). See panel E for a schematic depiction of the model. (A) Flash suppression followed by a period of regular binocular rivalry. (B) DR paradigm. The gated activity demonstrates how the activity corresponding to the remaining stimulus is temporarily blocked due to the transient removal of the flash stimulus. (C) CT paradigm. A period of blocked activity is not present when the adaptor stimulus is removed during the presentation of the flash stimulus. (D) DRE during continuous binocular rivalry. One of two stimuli is switched off abruptly. Results are shown for conditions in which the removed stimulus was dominant at the time of removal (DOM) and suppressed (SUP). Clear DRE is present in the gated signal. (E) Schematic depiction of the model. Populations of transient-selective neurons (T1 and T2) detect changes in stimulation of the two eyes (E1 and E2). A contrast (TC) between the transient signals detected in each eye is calculated. If TC crosses a threshold (here 0.75), it evokes a gating mechanism by which only the sustained eye information corresponding to the same eye as the most active population of transient neurons is made available for further processing. Sustained activity corresponding to the other eye is blocked by this mechanism.

participants generally reported perceiving the background color presented to the eye without a stimulus element during DRE (Experiment 4).

Our computational model could reproduce the main DRE results, building on binocular rivalry principles. The model needed to implement a crucial role for visual transients in determining conscious percepts during rivalry. Indeed, stimulus onset *and* offset are known to lead to neuronal responses in early visual regions (e.g., Macknik & Livingstone, 1998). These transient onset and offset neurons can "boost" the representation of the transient-receiving eye and influence its competition with the other (transient-free) eye. Indeed, also in the context of binocular rivalry, influences of transients and attention on perceptual dominance have previously been reported (Ooi & He, 1999). The rivalry interpretation of DRE seems to suggest that, after these transient-induced boosts, DRE is a case of predominantly eye-based dominance because there are no

rivaling patterns at this point. As such, it represents an interesting phenomenon for the ongoing debate on the relative contributions of rivaling monocular channels and image representations in binocular rivalry (e.g., Blake & Logothetis, 2002; Brascamp, Sohn, Lee, & Blake, 2013; Logothetis, Leopold, & Sheinberg, 1996).

Although the competing physical stimulus is absent from the onset of DRE onward, it would be premature to state the same about all neuronal representation of the flashed rivalry stimulus. Although the eye may not receive further inputs, is this true for the "eye channel" in its entirety? Recent studies have shown that afterimages can engage in rivalry with real images (Bartels, Vazquez, Schindler, & Logothetis, 2011; Gilroy & Blake, 2005). Perhaps the removed stimulus in the DRE paradigm induces an afterimage on the perceptual, or at least "neural," level, which could theoretically compete with and suppress the adaptor stimulus. In that regard, it is important to note that (a)

although we did informally observe afterimages in some implementations of the paradigm, they did not seem as salient as the remaining adaptor stimulus; (b) longer rivalry stimulus presentation (presumably leading to stronger afterimages) actually evoked shorter DRE durations (Experiments 1 and 2); (c) it seems unlikely that a flashed rivalry stimulus of only a few hundred milliseconds would induce an afterimage that is strong enough to suppress a sustained salient stimulus for up to several seconds; and (d) although we did not systematically explore this, informal observations suggest that a monocularly presented peripheral stimulus could also spontaneously disappear, in which case a rivaling afterimage never appeared. Nevertheless, the potential role of negative afterimages in DRE invites further experiments.

One challenge for the rivalry interpretation of DRE lies with the considerably long durations of the disappearance effect (see computational models 2 and 3 in the Supplementary Material). Also, the predicted influence of adaptation duration on DRE duration was only weakly supported by our experimental results. Therefore, there may be additional mechanisms at play in DRE. In line with this, our computational modeling showed that binocular rivalry mechanisms alone could not account for perceptual suppressions lasting as long as sometimes observed in DRE. What other disappearance paradigms might be related to DRE?

Fading (possibly related to "filling in," Weil & Rees, 2011) is the disappearance of a peripheral stimulus after some time of stable fixation (Troxler, 1804). In recent years, it has been demonstrated repeatedly that a visual transient can induce fading in a time-locked manner (Breitmeyer & Rudd, 1981; Kanai & Kamitani, 2003; May, Tsiappoutas, & Flanagan, 2003; Moradi & Shimojo, 2004; Simons et al., 2006). "Generalized flash suppression" (GFS, Wilke et al., 2003, discussed further below) also induces disappearance of a peripheral stimulus without local interocular conflict and has been shown under both monocular and binocular viewing conditions. Visual transients have been shown to not only induce time-locked fading, but also perceptual reversals (Kanai, Moradi, Shimojo, & Verstraten, 2005). So a common denominator in several paradigms appears to be the induction of a new perceptual state by a visual transient, which can make a peripheral stimulus disappear for several seconds. Is DRE then fully explained by transient-induced fading? Perhaps not, because fading generally seems to involve weak, low-contrast stimuli without sharp edges and because results from Experiment 4 suggest that visual awareness represents the unstimulated eye during DRE as opposed to the stimulated eye in which the stimulus element has faded. Our current interpretation of DRE and our computational model integrate elements of binocular rivalry mechanisms and percept-stabilizing mechanisms possibly involved in other disappearance paradigms.

DRE: Working model

Our computational model reproduced our main behavioral results by implementing a powerful role of visual transients (onsets *and* offsets) in a reciprocal inhibition framework coupled with a selection mechanism "upstream" in the visual hierarchy. This "gating mechanism" resembles attention-based gating of preconscious processing streams. In this context, the transient events in our experiments can be thought of as salient events that attract a very low-level form of attention and evoke a similar gating mechanism, which then determines which eye/stimulus signal is "connected" to upstream processing. The gating mechanism thus essentially functions as a stabilizing mechanism that temporarily "sticks with one of two eyes" for perception when nothing further in the visual scene changes (i.e., no transients).

Kanai and colleagues (Kanai, Carmel, Bahrami, & Rees, 2011; Kanai & Kamitani, 2003; Kanai, Muggleton, & Walsh, 2008) have suggested that a stabilizing signal, attentional boost, or percept maintenance function may be instantiated by a recurrent loop between early visual areas and the parietal cortex. Brain stimulation of the parietal cortex can affect binocular rivalry (Carmel, Walsh, Lavie, & Rees, 2010; Kanai, Bahrami, & Rees, 2010; Kanai et al., 2011; Zaretskaya, Thielscher, Logothetis, & Bartels, 2010), and single transcranial magnetic stimulation pulses to the parietal cortex can induce perceptual fading of contralateral targets (Kanai et al., 2008)—two sets of observations in line with this idea. A neural loop that stabilizes the current percept could be reset by strong visual transients, explaining not only transient-induced fading, but also transient-induced perceptual alternations in bistable vision (Kanai et al., 2005) and possibly also (part of) DRE.

In sum, (eye-based) binocular rivalry mechanisms in a reciprocal inhibition model—boosted by visual (offset) transients—may explain the initial existence of DRE. The concept of a transient-sensitive stabilizing mechanism may then explain long durations of DRE. It might moreover link DRE to other disappearance phenomena. In fact, one might speculate that the transient-sensitive stabilizing mechanism may be common to many disappearance paradigms. Many perceptual disappearance paradigms (see Breitmeyer, 2015, for a recent review) are characterized by disappearance durations "in the order of seconds." Among these paradigms and aside from transient-induced fading, GFS may perhaps have most in common with DRE (Wilke et al., 2003; Wilke, Mueller,

& Leopold, 2009). In GFS, a very salient visual stimulus is presented around a peripheral target, causing it to subsequently disappear from perception. In a dichoptic setup, this suppression effect is increased if the target stimulus is in one eye and the surround stimulus in the other eye. Similar to DRE, GFS essentially involves sustained suppression of a salient peripheral target stimulus in the absence of local inter- or intraocular conflict. However, although the underlying mechanisms of DRE and GFS may partially overlap, there is also an important difference between the two paradigms. In GFS, as well as in nearly all other paradigms that induce perceptual disappearance of a salient peripheral stimulus, the "suppressing" stimulus remains present during perceptual disappearance of the suppressed stimulus whereas in DRE perceptual disappearance occurs in the absence of a suppressing stimulus.

This difference highlights the potential methodological value of DRE in the search for neural correlates of visual awareness. DRE involves the controlled disappearance and then spontaneous reappearance of a salient visual stimulus to awareness without any concurrent distracting stimulation anywhere in the visual field (except the fixation dot and fusion-guiding frames). One may even argue that there is no real suppressing agent for most, if not all, of the disappearance duration. Yet the onset of perceptual disappearance is under full experimental control. One paradigm that seems related in these respects is the recently introduced contour adaptation paradigm (CA, Anstis, 2013). In the CA paradigm, contour adaptation is evoked by rapidly and saliently flashing the outlines of a shape (i.e., the edges) prior to the presentation of the shape itself. Interestingly, this causes the shape to not be consciously perceived for up to several seconds. Neither CA nor DRE require a persistent visual suppressor during the disappearance duration, making both these paradigms highly suitable to study visual awareness, for instance, with neuroimaging (Cox et al., 2014).

Conclusion

We have explored DRE as a visual phenomenon with potentially powerful theoretical and methodological implications. Computational modeling on the basis of behavioral results suggests a potential mechanism for DRE involving visual onset and offset transients as determinants of a transient-sensitive gating mechanism. Once an eye channel is selected by this mechanism, it remains dominant in determining the content of visual awareness for up to a few seconds. Transient-induced prioritization of sensory processing for conscious perception seems an efficient mechanism to keep track of unexpected changes in the environment, and it would be an interesting objective for future studies to explore the general validity of such a mechanism beyond the paradigms used in the current study. Methodologically, the phenomenon and its controlled implementation reported here might be very valuable for neuroimaging studies. Several such studies are currently in progress.

Acknowledgments

Footnotes

[1] Removed prior to analysis because of consistent failure to properly indicate the current percept by releasing one of two mouse buttons. This made it impossible in a substantial number of trials to determine which images were perceived at which time. Other participants had no such problem.

[2] This model was originally developed to explain the "perceptual stabilization" effect that occurs when the presentation of rivalry stimuli is interrupted by intermittent blank periods (Brascamp et al., 2008; Leopold, Wilke, Maier, & Logothetis, 2002; Noest et al., 2007; Orbach, Zucker, & Olson, 1966; Pearson & Brascamp, 2008; van Ee, 2009). To account for this effect during intermittent presentations, the model contains a parameter β that can be discarded in the case of continuous rivalry.

[3] Simulations of this model and all other variants were performed with parameters $\alpha = 6$, $\gamma = 5.25$, and $\tau = 50$, and stimulus amplitudes E1 and E2 varied between zero and one with white noise added (power = 5×10^{-5}).

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