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Inattention Abolishes Binocular Rivalry: Perceptual Evidence

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Abstract

Binocular rivalry refers to the unstable perceptual experience that arises when an observer views a different image with each eye: Each image reaches awareness in turn as the other becomes temporarily invisible. Using a novel experimental paradigm, we provide the first direct, perceptual evidence that binocular rivalry occurs only in the presence of attention. Observers in our experiment withdrew attention from a binocular rivalry stimulus shortly after one of the eyes' images was forced to visibility. Seconds later, they shifted attention back to the stimulus to report their perception. For all observers, reported perception strongly and significantly deviated from the results that would be expected if binocular rivalry continued during inattention. Strikingly, reports instead exactly matched those obtained when the stimulus was physically removed for seconds rather than left unattended. These results show that disregarding a binocular rivalry stimulus is equivalent to having it removed from view. Thus, inattention abolishes binocular rivalry.

Keywords

attention, perception, visual attention, binocular rivalry, visual perception

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Binocular rivalry is the intriguing perceptual phenomenon that arises when each eye is shown a very different image. Instead of experiencing the usual stable view of the world, the observer experiences fluctuating perception wherein the two images compete for dominance, with the losing image temporarily vanishing from awareness (Blake & Logothetis, 2002). A topic of scientific research for well over a century, binocular rivalry has enjoyed more intense interest in recent years, partly as a tool for investigating the neural basis of conscious experience (Crick & Koch, 1998).

In the study reported here, we investigated whether binocular rivalry's cycle of alternating dominance and suppression still occurs when attention is withdrawn from the rival images. Interest in the relation between binocular rivalry and attention is almost as old as binocular rivalry research itself (Helmholtz, 1859/1910), owing in part to the conceptual similarity between binocular rivalry's perceptual switches and attention's shifts in perceptual focus (Leopold & Logothetis, 1999). Recent studies have increased researchers' understanding of this relation by showing that attention affects the dynamics of binocular rivalry (Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999; Paffen, Alais, & Verstraten, 2006; Paffen & Van der Stigchel, 2010). Moreover, human brain imaging has revealed activation of similar brain areas in attention switching and in binocular rivalry (Knapen, Brascamp, Pearson, van Ee, & Blake, 2011; Lumer, Friston, & Rees, 1998; Sterzer, Kleinschmidt, & Rees, 2009).

Despite this growing understanding of the involvement of attention in binocular rivalry, the most fundamental question remains elusive: Can binocular rivalry even exist without attention? Two earlier studies employed indirect measures to get at this question. In both studies, observers withdrew attention from a binocular rivalry stimulus, in one case while researchers measured electrophysiological signals evoked by the rivalry stimulus using scalp electrodes (Zhang, Jamison, Engel, He, & He, 2011) and in the other during magnetic resonance imaging (Lee, Blake, & Heeger, 2007). Results from the first study suggested that binocular rivalry is absent without attention, but results from the other one implied that rivalry did continue. We sought to resolve the issue by taking a different approach. Instead of measuring binocular rivalry indirectly via concomitant signals, we directly assessed the perceptual consequences of inattention to rival stimuli using a novel paradigm.

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An obvious difficulty in measuring perceptual effects of inattention is that the observer cannot report perception of the stimulus while fully attending elsewhere. To solve this problem, we capitalized on the fact that perception during binocular rivalry, although variable, has some degree of predictability. Using this predictability to our advantage, we measured the perceptual consequences of withdrawing attention from a binocular rivalry stimulus.

Method

Background

Durations of individual dominance periods during binocular rivalry cluster around a mean, such that durations close to the mean are much more likely than shorter or longer ones (Levelt, 1967). Thus, knowing which image an observer currently perceives allows one to predict which one will likely dominate a given time interval later, provided that binocular rivalry has continued in the intervening period. Conversely, the relation between perception before and after an intervening period allows one to assess whether binocular rivalry occurred during this period, even if perception is not reported during the period itself.

Our basic approach was to quantify, in an *unattended* condition, the relation between perception before and after a period of inattention, and then to compare the results with those obtained in two other conditions. In the first comparison condition, the *attended* condition, observers simply attended to the rivalry stimulus continuously, even throughout the period that had been marked by inattention in the unattended condition; the attended condition thus revealed the temporal characteristics of the perceptual sequence of binocular rivalry. In the second comparison condition, the *absent* condition, the period of inattention was replaced by a period of physical stimulus removal, so that binocular rivalry did not take place during that time. In principle, perception in the unattended condition might fall anywhere between the extremes observed in the comparison conditions, as inattention might weaken or modify binocular rivalry without abolishing it. However, to preview our results, our data showed no such intermediate pattern. Instead, results for the unattended condition exactly matched those for the absent condition in all analyses while deviating markedly from results for the attended condition, a pattern indicating that binocular rivalry without attention is equivalent to no binocular rivalry at all.

Procedure

Seven healthy naive observers (5 females, 2 males; ages 21–36 years) participated. All had normal or corrected-to-normal vision and gave written informed consent. The experiment conformed to the local ethics guidelines.

Figure 1a schematically illustrates our trial sequence. We dictated perceptual dominance at trial onset using *flash suppression* (Wolfe, 1984), a procedure wherein binocular rivalry is preceded by presentation of one of the rival images in isolation, without its counterpart (Phase I). This caused the counterpart to become dominant when it was added to produce binocular rivalry. The next phase (Phase II) differed between conditions. In the unattended condition, the counterpart was added simultaneously with the onset of a fast sequence of letters at fixation (rapid serial visual presentation, or RSVP). Observers counted the occurrence of target letters, which forced them to disregard the binocular rivalry stimulus, which was presented outside of fixation. In the attended condition, visual stimulation was the same, but observers ignored the RSVP stream, instead reporting perception of the rivalry stimulus, pressing a different keyboard key to indicate the onset of perceptual dominance of each of the two rivalry images. In the absent condition, observers again counted target letters in the RSVP stream, but no rivalry stimulus was present. Instead, a neutral, nonrivalry stimulus occupied its location. The final phase of each trial (Phase III) was again identical across conditions: The RSVP stream ended, and observers either started or continued to report their perception of the binocular rivalry stimulus. In the attended and unattended conditions, this stimulus had been there all along; in the absent condition, the nonrivalry placeholder was quickly replaced by a rivalry stimulus at the moment the RSVP stream ended.

Figure 1b shows the trial sequence in detail, taking the unattended condition as an example. Our rivalry stimulus consisted of a pair of Gabor patches (spatial frequency = 2 cycles/°; maximum contrast = 50%; $\sigma = 0.39°$; average luminance = 46.8 cd/m^2, equal to background luminance), oriented +45° and −45° from vertical in the two eyes, respectively. During Phase I, we randomly showed either of these two Gabor patches in isolation. On each trial, the stimulus appeared randomly at one of six positions spaced evenly on an imaginary circle (radius = 2.5°) around fixation (the 12 o'clock position in Fig. 1b). During Phases I and II, the remaining five positions were occupied as well, but by stimuli irrelevant to the task; the purpose of these stimuli was to prevent deployment of attention to the binocular rivalry stimulus, as a single stimulus in isolation may draw attention despite a concurrent task (Mack & Rock, 1999). During Phase I, these irrelevant stimuli were monocular gratings just like the relevant stimulus (their orientation and the eye to which they were presented alternated between adjacent stimuli during this phase; see Fig. 1b); during Phase II, the irrelevant stimuli were fusible Gabor patches, randomly oriented horizontally or vertically. As a further precautionary measure, we slid the binocular rivalry stimulus (and the five irrelevant stimuli) slowly around the circle during Phase II (direction of movement was randomly assigned), so that by the time observers attended to the rivalry stimulus in Phase III, it occupied a retinal position not differentially adapted during flash suppression. This ruled out any direct effects of lingering adaptation on perception following inattention, because such adaptation is tied to the retinal location where it was induced (e.g., Blake, Sobel, & Gilroy, 2003; Carter & Cavanagh, 2007). A control experiment demonstrated that our results did not critically depend on this

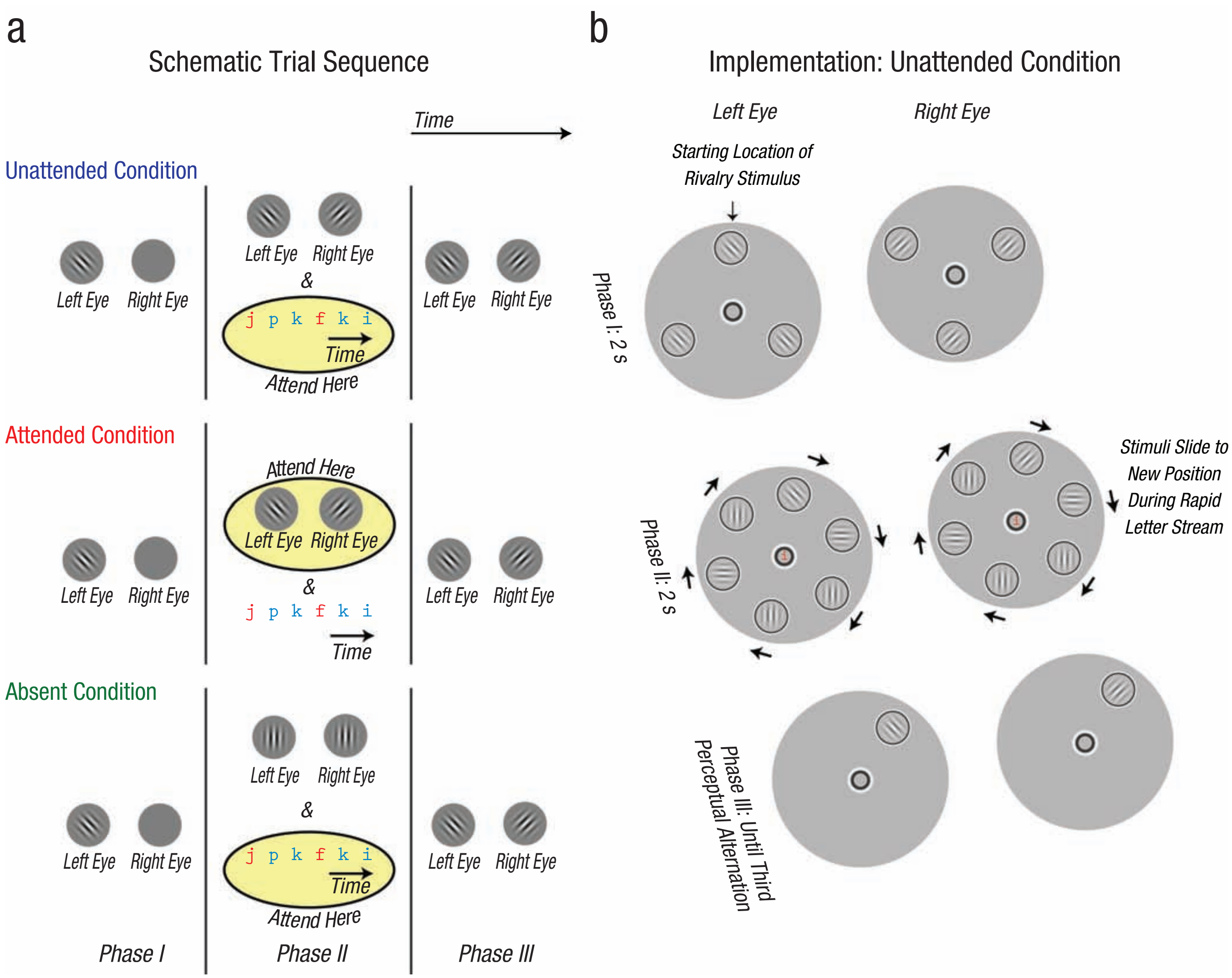

Fig. 1. Trial sequence: (a) schematic overview of the three conditions and (b) detailed illustration of the sequence in the unattended condition. Each condition began with presentation of one of the rival images in isolation (Phase I). Next (Phase II), either the second half of the rival display was added (unattended and attended conditions) or the image was replaced by a neutral nonrivalry stimulus (absent condition). Simultaneously with this change, a rapid stream of sequentially presented letters began at fixation. Finally (Phase III), this stream of letters ended, while the rivalry stimulus continued to be presented (unattended and attended conditions) or was introduced (absent condition). In the unattended condition (b), the rivalry stimulus appeared randomly at one of six positions spaced evenly on an imaginary circle. During Phase I, the remaining five positions were occupied by monocular gratings irrelevant to the task. During Phase II, these positions were occupied by irrelevant, fusible Gabor patches, and all stimuli slid slowly around the circle. During Phase III, only the rivalry stimulus remained. The other conditions were implemented analogously (see the text for details).

displacement (see Additional Control Conditions in the Supplemental Material available online). Phases I and II both lasted 2 s, and Phase III lasted until the third perceptual alternation was reported.

The letters in the RSVP stream (approximately 0.3° × 0.2°) were randomly presented in either red or blue. During unattended and absent trials, observers counted the total number of red *k*s and blue *j*s and reported at the end of each trial whether this number was odd or even, receiving feedback. To ensure maximal attentional demand, we continually adjusted the time interval between consecutive letters using a 1-up/2-down staircase, so that letters appeared in faster succession whenever performance improved.

The other two conditions were implemented analogously. Thus, the absent condition involved six fusible stimuli instead of five during Phase II (each oriented horizontally or vertically) but was otherwise identical to the unattended condition, whereas the attended condition differed from the unattended condition only in the fact that a small dial pointed to the rivalry stimulus during Phase II, to help the observer find this stimulus and track perception. Each observer completed about 150 trials per condition.

Each observer completed several 20-min sessions of trials. Although attended trials were presented in separate sessions (so that the instructions given to observers did not change within sessions), the unattended and absent trials were randomly interleaved within sessions. If observers directed their attention exclusively to the RSVP stream, as instructed, these latter two trial types should have been subjectively indistinguishable during these sessions. To verify that they were, we instructed observers to press a separate button if they happened to notice a rivalry target during Phase II (i.e., any target containing diagonal orientations) despite the fact that performance on the RSVP task had priority. Observers rarely pressed this button (on 1.2% of trials on average; these trials were discarded), and did so as often on unattended trials as on absent trials, which indicates that these were indeed indistinguishable.

Analysis

Percept durations differ systematically across retinal locations (Chen & He, 2003) and observers (Carter & Pettigrew, 2003). To prevent signals from different locations and observers from canceling each other out in our analyses underlying Figures 2b through 2d, we normalized our time axis by dividing elapsed time by the average percept duration for each combination of observer, retinal starting location, and slide direction (cf. Fig. 1b). To determine significance for individual observers' data for a given condition, we used a bootstrap procedure based on reshuffling, implemented as follows. By design, each observer performed an even number of trials for each combination of flash-suppression orientation, starting location, and slide direction. In the analysis of our actual (nonreshuffled) data, we sorted each observer's data by flash-suppression orientation such that perceived grating was defined as either the same as or orthogonal to this orientation. However, on every repetition of the reshuffling procedure, we instead made a random selection, for each starting location and slide direction, of half of the trials that used one flash-suppression orientation and half of those that used the other orientation, subsequently continuing the analysis as if all trials used the same orientation. In this procedure, any effects of flash suppression, if present, cancel out, so that the range of signal strengths expected without any flash-suppression effects is revealed. By comparing the signal in the actual (nonreshuffled) data of a given observer and condition with the distribution of signal strengths observed across repetitions of this reshuffling procedure, we could then calculate whether this signal deviated significantly from the expectation in the absence of flash-suppression effects.

Results

Figure 2a summarizes a typical observer's perceptual reports. It shows the proportion of trials on which the initially forced image dominated as a function of normalized time within a trial, the initially forced image being the one whose initial dominance we promoted using flash suppression (this could be either image). This observer's results from the attended condition demonstrate that flash suppression often successfully dictated initial perception, as the curve starts high. More important, echoes of the flash-suppression procedure were still evident further into the trials: The approximate periodicity of the perceptual cycle ensured that the initially forced percept was usually suppressed a short time after its initial dominance (the curve falls below .5), and often regained dominance a while later. These echoes are of interest because they continued well after Phase II and should therefore also have been measurable following inattention, provided that rivalry continued during inattention. Even when we tested only the part of the curve to the right of the vertical line in Figure 2a (i.e., after Phase II; accounting for reaction time by shifting all time points by an estimated reaction time of 400 ms, based on Van Dam & Van Ee, 2006), these echoes were highly significant ($p < .01$ based on the reshuffling procedure described in the Method section).

In the absent condition, this observer's curve starts later because no rivalry was reported during Phase II. When reports began later, no echoes of flash suppression were evident ($p > .5$). This is as expected because these echoes depend entirely on continuation of the perceptual alternation cycle, which cannot occur during stimulus absence.

The unattended condition for this observer again provided no data for Phase II, because the observer was performing the RSVP task. More important, when the observer did start to report perception, this analysis revealed no trace of the flash-suppression procedure ($p > .5$), mirroring the results in the absent condition. In other words, at any moment during the unattended trials, this observer was as likely to perceive the initially forced image as the other image, despite the fact that results for the attended condition demonstrated that this should not have been the case if binocular rivalry had continued. This analysis provides evidence that binocular rivalry did not continue while the observer attended elsewhere.

Note that a mere change in the temporal dynamics of binocular rivalry outside of attention does not explain this outcome in the unattended condition. For instance, if the dominance cycle remained, yet slowed down during RSVP (as during partial attention withdrawal; Paffen et al., 2006), this would have resulted in a rightward shift of the signal seen in Figure 2a, rather than its disappearance.

Figure 2b shows results averaged across observers. Again, data from the attended condition showed clear effects of flash suppression even when Phase II was excluded from analysis, but data from the absent condition and the unattended condition did not. Only the attended condition produced data points that deviated significantly from .5 (two-tailed t test, $p < .01$; see Fig. 2b).

Figure 2c shows the strength of perceptual signals in the absent condition, the benchmark for abolished binocular rivalry, as a function of the strength of perceptual signals in the attended condition and the unattended condition. We quantified these perceptual signals for each observer as the root-mean-square distance between perception curves like those of Figure 2a and the .5 line. This measure is thus sensitive to any perceptual tendency consistently linked to the flash-suppression procedure, regardless of its direction or timing.

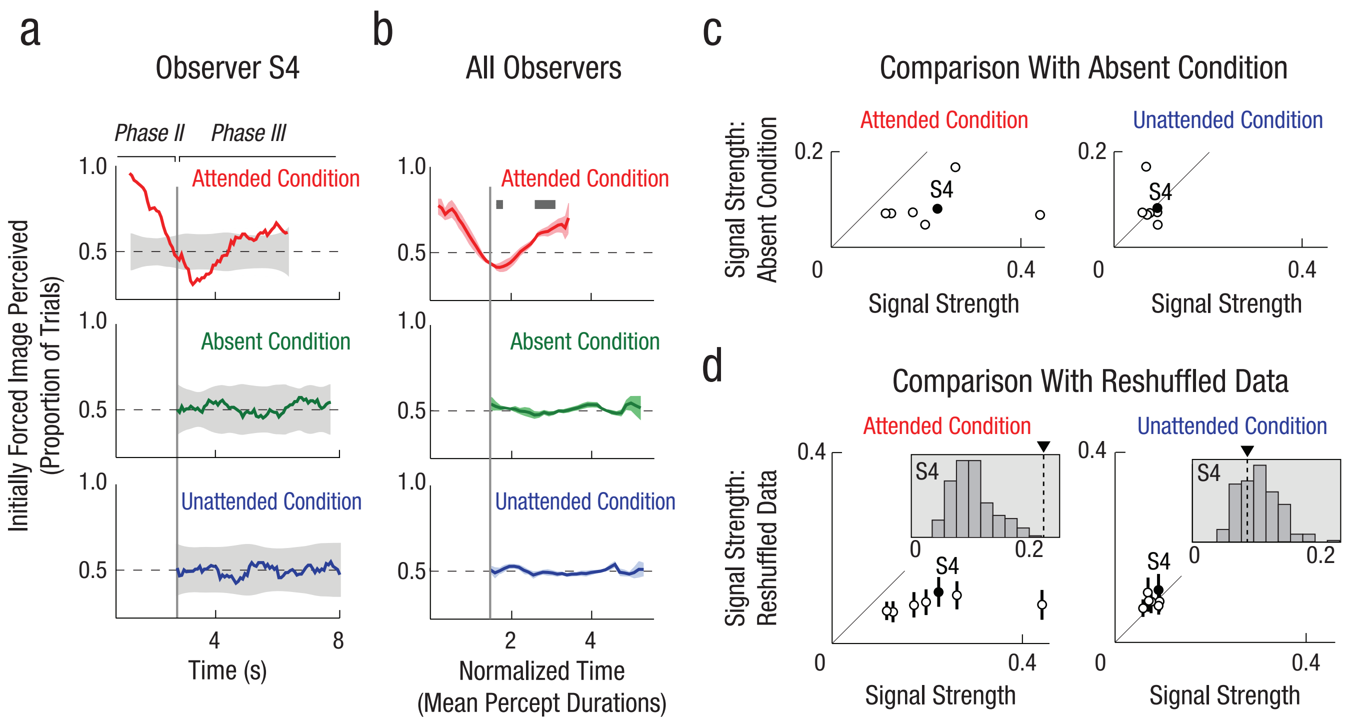

Fig. 2. Experimental results. The line graphs show the proportion of trials on which the initially forced image dominated as a function of time within a trial (normalized time in the case of panel b), separately for the three conditions. Results for a single observer are shown in (a). In these graphs, results are plotted only for time points for which more than 50% of trials provided data (thus, data at the start and end of some trials were excluded). Moreover, only the attended condition provided data for Phase II (left of the vertical gray line). The gray shading indicates 95% confidence intervals for signal absence, obtained from a reshuffling procedure (see the Method section). Results averaged across all observers are shown in (b). In these graphs, results are plotted only for time points for which at least 3 observers provided data. The colored shading indicates 1 standard error of the sample mean. The gray bars above the curve for the attended condition indicate data points that deviated significantly from .5 (two-tailed *t* test, $p < .01$). The scatter plots in (c) show signal strength in the absent condition, which could show no echoes of flash suppression, as a function of signal strength in the attended (left) and unattended (right) conditions. The scatter plots in (d) show signal strength as measured by reshuffled data (in which echoes of flash suppression are canceled out; see the text) as a function of signal strength in the actual (nonreshuffled) data, separately for the attended and unattended conditions; the insets show, for 1 observer, the frequency distribution of the signal strengths obtained in repetitions of the reshuffling procedure (histograms) and the signal strength in the actual data (dashed line).

For each observer, signal strength was greater in the attended condition (counting only data beyond Phase II, taking into account an estimated reaction time of 400 ms) than in the absent condition; there was a significant difference between these conditions across observers, $t(6) = 3.3$, $p = .02$ (two-tailed paired *t* test). This result confirms the presence of a signature of ongoing rivalry in the attended condition. However, signal strength did not differ between the unattended and absent conditions, a result consistent with the notion that binocular rivalry did not occur during inattention, $t(6) = 0.31$, $p = .77$ (two-tailed paired *t* test). An analogous comparison between the attended and unattended conditions (not shown in Fig. 2c) did reveal a difference, $t(6) = 3.3$, $p = .02$ (two-tailed paired *t* test).

Figure 2d uses a different no-rivalry benchmark: the signal strength in data that have been reshuffled such that any effects of flash suppression are canceled out (see the Method section). This approach has the benefit of allowing within-observer statistical tests. The scatter plots show, for each observer, the signal strength in the reshuffled data as a function of signal strength in the actual data, separately for the attended and unattended conditions. When the data were assessed in this manner, each observer showed a significant signal in the attended condition ($p < .01$ for 5 observers, $p < .05$ for the remaining 2), and no observers showed a significant signal in the unattended condition ($p > .10$ for each observer).

Although no effects of the flash-suppression procedure could be discerned following stimulus absence (i.e., in the absent condition; Fig. 2), perception was not random. Results were consistent with previous work (Carter & Cavanagh, 2007; Stanley, Carter, & Forte, 2011) in that there were systematic tendencies to perceive a particular image first upon stimulus appearance, and these biases differed among observers and retinal locations. Interestingly, biases for the first percept following inattention in the unattended condition were strongly correlated with those following stimulus absence (linear regression including 42 observer-location combinations: slope = 0.71, adjusted $r^2 = .58$, $p < .01$). This again points to equivalence between the unattended and absent conditions, and the presence of these systematic patterns that are in line with the existing literature also confirms that our observers reported their perception reliably.

In summary, perception following unattended rivalrous stimulation is consistently different from perception following attended rivalry, yet indistinguishable from perception following stimulus absence. This suggests that binocular rivalry does not occur without attention.

Figure 3 shows results of analyses complementary to those of Figure 2. These additional analyses were not concerned with which image was dominant at a given moment (and, incidentally, were not dependent on whether flash suppression was successful), but instead focused on the moment at which dominance changed. Figure 3a illustrates the approach. In the absent condition, binocular rivalry started at the beginning of Phase III, and the first perceptual alternation occurred about one average percept duration later. In the unattended condition, the situation is very similar if one assumes that inattention abolishes binocular rivalry; rivalry would start at the beginning of Phase III, and perception would change about one average percept duration later. In contrast, if inattention leaves binocular rivalry intact, Phase III would usually start during an ongoing dominance phase in the unattended condition, and the first perceptual alternation would often occur relatively soon after. Therefore, we tested for rivalry during inattention by investigating the timing of the first perceptual alternation reported following inattention.

The top graph in Figure 3b shows the distribution of times at which 1 observer reported his first perceptual alternation in the unattended and the absent conditions. These distributions were not significantly different (two-tailed Kolmogorov-Smirnov test on cumulative distributions: $D = .09$, $p = .82$), and consequently provided no evidence for binocular rivalry during inattention. Analyzing data from each of our 7 observers in this fashion, we found that the distributions in these two conditions differed significantly for only 1 of them, $p = .04$, not corrected for multiple comparisons; p values for the other observers ranged from .08 to .88, again providing little evidence for rivalry during inattention.

This analysis is sensitive to any kind of timing difference, including differences that are not even consistent with the hypothesis of binocular rivalry during inattention. Thus, we next tested specific predictions. The bottom left graph in Figure 3b compares the average moment of the first reported perceptual alternation between the unattended and absent conditions.

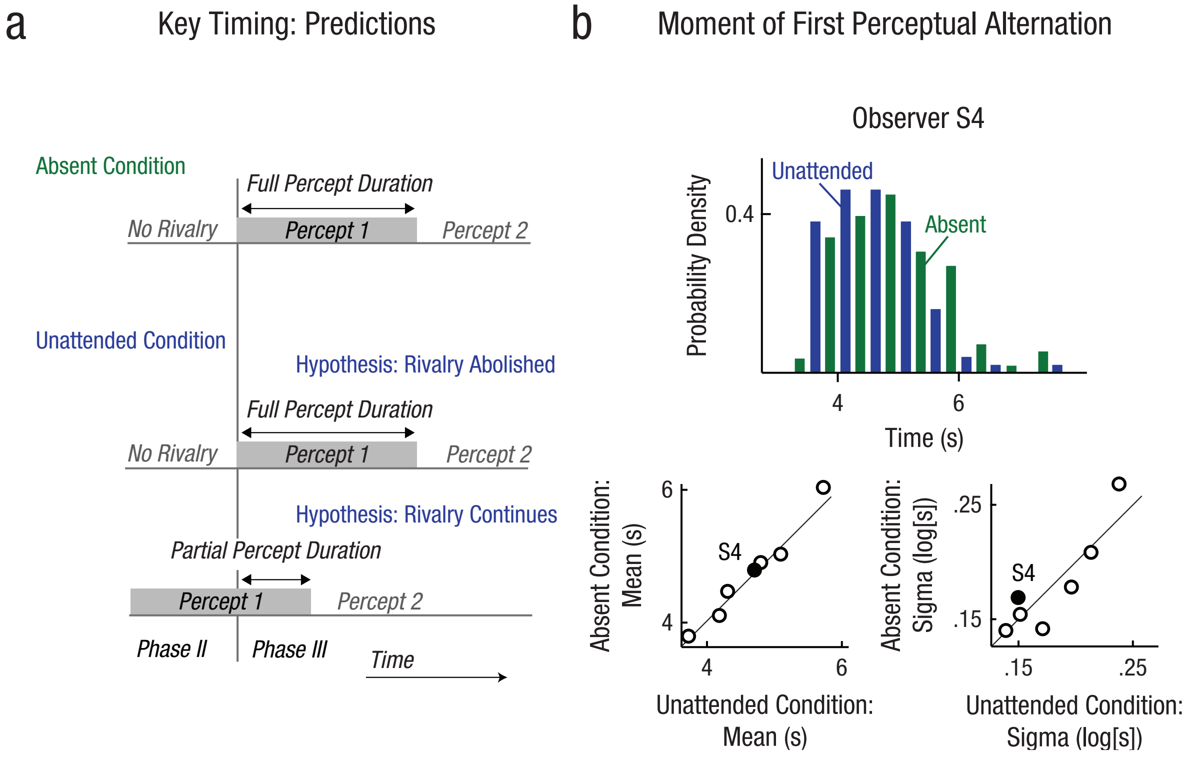

Fig. 3. Key timing analysis. As illustrated in (a), if inattention abolishes binocular rivalry, then binocular rivalry in the unattended condition cannot start until the beginning of Phase III, as in the absent condition. As a consequence, the first alternation of perception in the unattended condition would be reported about one average percept duration after the start of Phase III. In contrast, if rivalry continues during inattention, Phase III would typically start during an ongoing dominance phase in the unattended condition, and the first perceptual alternation would occur relatively soon thereafter. The histogram (b) shows, for 1 observer, the distribution of the timing of the first perceptual alternation (in seconds, counting from the start of Phase II) in the unattended and absent conditions (see the text for additional results). The scatter plots (b) show mean timing of the first perceptual alternation in the absent condition as a function of mean timing of the first perceptual alternation in the unattended condition (left) and variability in timing of the first perceptual alternation in the absent condition as a function of variability in timing of the first perceptual alternation in the unattended condition (right).

We found no difference, $t(6) = 1.95$, $p = .10$ (two-tailed paired *t* test), contrary to what would be expected if rivalry occurred without attention. The bottom right graph in Figure 3b compares the variability in timing of this same report. If binocular rivalry alternations occurred without attention, this spread would be larger in the unattended condition, because timing becomes increasingly unpredictable as rivalry progresses (i.e., separate trials are fully entrained at their onset but then run increasingly independent courses). Contrary to this prediction, we found no difference between the unattended and absent conditions, $t(6) = 0.01$, $p = .99$ (two-tailed paired *t* test).

To verify the reasoning behind these timing analyses, we compared the timing of the first perceptual alternation in the absent condition with the timing of the first perceptual alternation to occur after the end of Phase II in the attended condition (heeding reaction time by shifting all key presses by an estimated reaction time of 400 ms). In this latter condition, we knew that rivalry occurred during Phase II. Indeed, these timing distributions were significantly different in all observers ($p < .01$ for 6, $p < .05$ for the remaining 1); moreover, the first perceptual alternation occurred later on average in the absent condition, $t(6) = 3.76$, $p < .01$, and variability in the timing of this alternation was smaller in the absent condition, $t(6) = 2.61$, $p < .05$. A parallel analysis revealed similar differences between the attended and unattended conditions: different distributions for all but 1 observer, $p < .01$ for 4, $p < .05$ for 2; different average timing, $t(6) = 3.48$, $p = .01$; and different variability, $t(6) = 2.65$, $p < .05$.

The data presented so far provide no indication of binocular rivalry without attention. Might this result be attributable to properties of our unattended condition other than the absence of attention to the rivalry stimulus? We can think of two such alternative accounts. First, one putative consequence of inattention is a reduction in effective stimulus contrast (Paffen et al., 2006; Reynolds & Heeger, 2009). Because rivalry can break up when stimulus contrast drops below a critical value (Liu, Tyler, & Schor, 1992), we wondered whether our findings might be attributable to the effective contrast of our stimuli being too low during inattention. To investigate this possibility, we repeated our attended condition while mimicking the effect of inattention by reducing stimulus contrast by half. This reduction left the signature of rivalry undiminished (see Additional Control Conditions and Fig. S1a in the Supplemental Material). Thus, reduced effective contrast was ruled out as the cause of the disappearance of the signature of rivalry in the unattended condition. A second alternative account centers on the finding that attention shifts can cause dominance switches in binocular rivalry (Paffen & Van der Stigchel, 2010). Could it be that binocular rivalry occurred during Phase II of the unattended condition, but that its traces were erased when observers then shifted attention toward the rivalry stimulus to track perception? To evaluate this possibility, we asked observers to track rivalry but then make a brief attention switch to fixation and immediately back to the stimulus to continue tracking. The results again showed a clear signature of rivalry despite the presence of these two attention shifts (see Additional Control Conditions and Fig. S1b in the Supplemental Material), indicating that attention shifts per se cannot explain our findings.

Discussion

We have shown that standard stimuli that cause robust binocular rivalry when attended do not elicit binocular rivalry when attention is withdrawn. Our results thus indicate that full attention withdrawal abolishes binocular rivalry, such that the rival images apparently receive an equal degree of processing, and the conflict posed by the visual input remains unresolved.

Our results are consistent with recent findings showing that concomitants of binocular rivalry measured using electroencephalography disappear when attention is withdrawn (Zhang et al., 2011), and also with preliminary findings (published in abstract form) on the perception of intermittently attended rivalry stimuli (Cavanagh & Holcombe, 2006; He, Jiang, & Chen, 2007). Our results may seem at odds, however, with a previous report that bistable perception can exist for two forms of ambiguous motion even when attention is distracted (Pastukhov & Braun, 2007). Although this apparent discrepancy may in principle reflect a difference between kinds of bistable perception, another explanation is that this earlier study may have allowed residual attention to the bistable stimulus despite the concurrent task. In line with that study's objective, its analyses were not primarily aimed at ruling out this possibility. Consistent with this explanation is the fact that observers in Pastukhov and Braun's study noticed dominance changes as they occurred, whereas our attention task was too demanding to allow such awareness (see the Method section). Our findings may also be unexpected in light of a functional MRI study that demonstrated V1 activity associated with dominance switches between unattended binocular rivalry images (Lee et al., 2007). In that study, however, dominance switches were exogenously triggered by a contrast increment within the rivalry stimulus, rather than endogenously caused, as was the case in our paradigm. Moreover, evidence suggests that the V1 signals in that study could be associated with neural processes that are engaged by rival stimulation but do not directly cause rivalry (Moradi & Heeger, 2009).

Why would binocular rivalry depend on the presence of attention? This question may be particularly pressing in the context of the common view of binocular rivalry as a product of inhibition between sensory representations combined with neural adaptation and noise (Alais, Cass, O'Shea, & Blake, 2010; Blake et al., 2003; Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Lankheet, 2006), a conceptualization formalized in computational models of the phenomenon (Moreno-Bote, Rinzel, & Rubin, 2007; Wilson, 2007). These models describe many aspects of binocular rivalry, yet rely exclusively on neural properties so automatic that variants are observed even in anaesthetized animals, in which attention is ruled out (Sanchez-Vives, Nowak, & McCormick, 2000;

Sengpiel, Blakemore, & Harrad, 1995). Although such models may accurately describe computations underlying binocular rivalry, our results raise the question as to how these are implemented in the brain to produce such profound dependence on attention.

As a tentative answer, we propose that attention plays a critical role in the neural competition process prompted by rival visual stimulation. Attention is often conceptualized in terms of competition between sensory representations (Desimone & Duncan, 1995; Reynolds & Heeger, 2009). In this conceptualization, attention biases the conflict that arises between representations along the visual processing stream, thus determining which signals proceed to subsequent processing stages, and ultimately influencing what reaches awareness (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Mack & Rock, 1999; Van Boxtel, Tsuchiya, & Koch, 2010). We suggest a related role for attention during binocular rivalry: Attention may amplify slight benefits that one representation might temporarily have over the other, and thereby bring about the winner-take-all nature of binocular rivalry, characterized by full dominance and suppression. There is considerable evidence that attention plays a role in binocular rivalry (Dieter & Tadin 2011; Leopold & Logothetis, 1999; Mitchell et al., 2004; Ooi & He, 1999; Paffen & Alais, 2011; Sterzer et al., 2009); our results indicate that this role is so fundamental that the very dominance and suppression that define binocular rivalry cannot exist without attention.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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