Exogenous attention and endogenous attention influence initial dominance in binocular rivalry

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Abstract

We investigated the influence of exogenous and endogenous attention on initial selection in binocular rivalry. Experiment 1 used superimposed ±45° gratings viewed dioptically for 3 s, followed by a brief contrast increment in one of the gratings to direct exogenous attention to that grating. After a brief blank period, dichoptic stimuli were presented for various durations (100–700 ms). Exogenous attention strongly influenced which stimulus was initially dominant in binocular rivalry, replicating an earlier report (Mitchell, Stoner, & Reynolds. (2004). Object-based attention determines dominance in binocular rivalry. *Nature, 429*, 410–413). In Experiment 2, endogenous attention was manipulated by having participants track one of two oblique gratings both of which independently and continuously changed their orientations and spatial frequencies during a 5 s period. The initially dominant grating was most often the one whose orientation matched the grating correctly tracked using endogenous attention. In Experiment 3, we measured the strength of both exogenous and endogenous attention by varying the contrast of one of two rival gratings when attention was previously directed to that grating. The contrast of the attended grating had to be reduced by an amount in the neighborhood of 0.3 log-units, to counteract attention's boost to initial dominance. Evidently both exogenous and endogenous attention can influence initial dominance of binocular rivalry, effectively boosting the stimulus strength of the attended rival stimulus.
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1. Introduction

When the two eyes view different stimuli, people typically perceive only one at a time, with the dominant stimulus switching from one to the other unpredictably (Levelt, 1965). Called binocular rivalry, this intriguing phenomenon has recently been widely studied, in part because of its relevance for understanding resolution of perceptual conflict (Blake & Logothetis, 2002). Binocular rivalry, ever since its initial, systematic description by Wheatstone (1838), has been compared to visual attention, for understandable reasons—there are obvious similarities between the two. Both involve an element of selection, in that only one stimulus among alternatives is singled out for complete perceptual processing. Moreover, normally conspicuous changes to a non-dominant stimulus or to an unattended stimulus may go completely undetected (Blake, Yu, Lokey, & Norman, 1998; Rensink, O'Regan, & Clark, 1997). Furthermore, one cannot willfully maintain dominance of one percept in rivalry indefinitely, and nor can one sustain attention on a single object for a prolonged period of time (Pillsbury, 1908).

Is it reasonable to consider binocular rivalry as one instance of a category of phenomena lumped under the rubric of visual attention? Many distinguished scientific figures have endorsed this view, including Helmholtz (1925) and James (1891), and contemporary research has revealed strong links between rivalry and attention. We know, for example, that attention can influence the rate of alternations during rivalry (Chong, Tadin, & Blake, in press; Lack, 1978; Meng & Tong, 2004; Meredith & Meredith,

1962; van Ee, van Dam, & Brouwer, 2005) as well as the susceptibility of a stimulus to suppression (Ooi & He, 1999).

In a recently published paper, Mitchell, Stoner, and Reynolds (2004) presented evidence that object-based attention could influence the initially dominant stimulus at the onset of binocular rivalry. Those investigators "cued" one of two oppositely rotating sets of dots by briefly replacing 60% of that set of rotational dots with an equal number of translating dots, and they found that the cued rotational dots were subsequently more likely to be dominant at the onset of rivalry. While highly suggestive, the Mitchell et al result could be attributable, at least in part, to differential stimulus adaptation during the cuing period of each trial prior to the onset of rivalry: the cued dots briefly stopped rotating and, instead, translated while the other dots continued rotating—this means that the non-cued motion was present for a longer period of time. It is known that differential adaptation to a stimulus reduces its effectiveness when viewed subsequently during rivalry (Blake, Sobel, & Gilroy, 2003; Blake, Westendorf, & Overton, 1980). Thus, we wondered to what extent Mitchell et al's results (2004) are attributable entirely to object-based attention—differential adaptation could play a role in the biasing effect they observed. Moreover, in their study Mitchell et al used a physical change in a stimulus to direct attention to that stimulus, a manipulation that presumably engages exogenous attention (Breitmeyer & Ganz, 1976; Yantis & Jonides, 1984). We felt it would be informative to learn whether endogenous attention, involving no change in physical stimulation, could influence initial selection in rivalry, particularly since there is evidence that exogenous and endogenous attention arise from different mechanisms (see review by Yantis, 1998).

Accordingly, the present study replicated and extended Mitchell et al's experiments, using a technique that avoided any contribution of differential adaptation. Moreover, we tested the effect of both exogenous and endogenous attention on initial dominance of binocular rivalry. Also, we used a nulling technique to assess the magnitude of attention's influence on rivalry, expressed in units of effective contrast. By way of preview, we find that both exogenous and endogenous attention reliably influence the initial state of dominance during binocular rivalry.

2. General methods

2.1. Observers

Eleven individuals, including the first author, participated in different combinations of the three experiments reported here. Five observers participated in Experiments 1 and 2, respectively. Four observers participated in Experiment 3a and three participated in Experiment 3b. All had normal or corrected-to-normal visual acuity and good stereopsis. Every aspect of this study was carried out in accord with the regulations of the Vanderbilt University Institutional Review Board and of the Department of Psychology at Yonsei University.

2.2. Apparatus

Stimuli were created using MATLAB in conjunction with the Psychophysics Toolbox (Brainard, 1997) and were presented on the screen of a linearized NEC 21″ monitor (Experiments 1a and 2) or a linearized Samsung 21″ monitor (Experiment 1b). In all experiments, the monitor frame rate was 75 Hz. Observers viewed the monitor through a mirror stereoscope, with the left eye seeing only the left half of the screen and the right eye seeing only the right half of the screen. Effective viewing distance was 96.5 cm, meaning that a pixel subtended approximately 0.02° of visual angle. The observer's head was stabilized by a chin and forehead rest. Average luminance of the display, including background, was 13.3 cd/m².

2.3. Procedure

All experiments followed the same general procedure, described as follows. At the start of each trial, the observer viewed two superimposed gratings presented simultaneously and identically to each eye (dioptic phase); it was during this period of non-rival, dioptic stimulation that attention could be directed to one of the two gratings, either exogenously or endogenously. Next, following a brief blank period, dissimilar gratings were presented separately to the two eyes (dichoptic phase); these two rival gratings were oriented ±45° from vertical. Following offset of the dichoptic gratings, the observer used the computer keyboard to make a three-alternative categorization judgment about the perceptual experience produced by the dichoptic gratings (with the three alternatives being +45 grating only, the −45 grating only or a mixture of the two). At least 32 trials were devoted to each condition tested in any given experiment.

3. Experiment 1: Exogenous attention

This first experiment employed the strategy, but not the exact procedures, of the Mitchell et al. (2004) experiment, wherein exogenous attention was directed to one of two stimuli, both of which subsequently comprised rival stimuli. Our procedure, which was designed to minimize the possibility of selective adaptation to one of the two stimuli during the cueing phase, utilized an abrupt, transient increment in contrast to one of two superimposed patterns to cue exogenous attention. From other work (e.g., Luck & Thomas, 1999; Muller & Rabbit, 1989), it is known that visual transients of this sort can effectively cue attention to a given stimulus. In a follow-up experiment we measured the effectiveness of this exogenous cue as a function of the time elapsing between cue offset and the onset of the dichoptic stimuli, the aim being to learn whether cueing's effect on rivalry behaves like exogenous attention under other conditions of transient cueing (e.g., Nakayama & Mackeben, 1989).

3.1. Stimuli

One frame of the dynamic stimulus appearing during the dioptic phase of each trial is shown in Fig. 1A. This stimulus—a "plaid"—comprised two superimposed ±45° sinusoidal gratings both identical in size ($1° \times 1°$), contrast (13.4%), and spatial frequency (5 cycles/deg). This dioptically viewed plaid was present for 3 s, and during this period the plaid pattern flickered in counterphase at 2 Hz to preclude formation of afterimages. At a given moment during
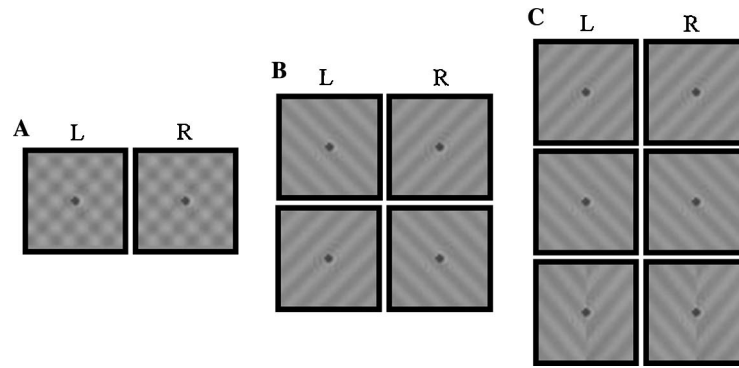
Fig. 1. The stimuli for Experiment 1. (A) Shows left and right eye gratings used during the dioptic phase of each trial. (B) Shows rival gratings for the dichoptic phase and (C) shows gratings for catch trials in the dichoptic phase. The figures are not drawn to scale.

this 3 s period, the contrast of one of the two gratings forming the plaid was abruptly incremented to the maximum value (13.4%) for 100 ms while the contrast of the other plaid component remained fixed at 4.5%; this brief, 0.47 log-unit contrast increment was constrained to occur only during the moment in time during the counterphase flicker cycle when both gratings were 4.5% in contrast. In Experiment 1a, this contrast increment always occurred at the end of the 3 s dioptic period; in Experiment 1b the 100 ms increment could occur either 200, 400 or 600 ms before the end of the 3 s period after which both dioptic components of the plaid were again equivalent in contrast and continued in counterphase flicker until the end of the 3 s period.

Conspicuous fusion frames (black contours, 0.12° in width) surrounded both gratings to stabilize binocular alignment of the two half-images; a small fixation circle (diameter: 0.08°) appeared within the center of the dioptically viewed gratings.

For the dichoptic phase of each trial, one of five possible pairs of test stimuli was presented to the two eyes on any given trial (alternatives are shown schematically in Figs. 1B and C). Two of these stimulus pairs constituted genuine rivalry trials, wherein the +45 and −45° gratings were presented separately to the two eyes (with the eye receiving +45° counterbalanced over trials)—these were the trials of actual interest. Also included were three types of 'catch' trials. On some catch trials both eyes received identical gratings oriented +45°, and on other trials the two eyes received identical gratings oriented −45°. On other catch trials, both eyes received a mock grating consisting of +45 and −45° parts, the aim being to mimic piecemeal rivalry (note: this mock stimulus viewed by both eyes was not a plaid but, rather, was a single grating consisting of two different orientations). Because there were objectively correct answers on the catch-trials, performance on these trials verified whether observers understood and followed the instructions. Catch trials were randomly intermixed with rival trials and they comprised 16% of the total trial number. The contrast of all the patterns used in the dichoptic phase was 13.4%. In both experiments, gratings present during the final moment of the dioptic period had the same

phase as the gratings presented during the dichoptic phase, thereby eliminating any possibility of perception of apparent motion between dioptic and dichoptic gratings.

3.2. Design

There were two independent variables in Experiment 1a, both of which varied within observers. The first variable was attention—on two-thirds of trials a 0.47 log-unit contrast increment was introduced to the +45 or to the −45° grating, and on the remaining one-third of trials no increment was introduced. This latter category of trial—no increment—was included to provide baseline measures of the incidence of initial dominance for the two rival orientations and of the incidence of mixtures. The second independent variable was the exposure duration of the dichoptic rival stimuli—100, 300, 500, or 700 ms. We included this manipulation as part of the replication of the procedure employed by Mitchell et al. (2004), who varied the exposure duration of the rival stimuli to trace the time-course of attentional cueing.

In Experiment 1b, there was one independent variable, cue lead time: the contrast increment happened at either 600, 400, 200, and 0 ms before the end of dioptic period. For this experiment, "no-cue" trials were excluded. The exposure duration of the rival gratings during the dichoptic phase was fixed at 250 ms, a value selected on the basis of results from Experiment 1a.

3.3. Procedure

On each trial observers first dioptically viewed the counter-phase flickering plaid whose contours were oriented ±45° relative to vertical. This dioptic phase lasted for 3 s, a duration deemed sufficiently long to preclude any effect of exogenous attention associated with the onset of the dichoptic stimulus itself. Observers were given no explicit attentional instruction other than to maintain fixation at the center of the plaid. At the end of the 3 s dioptic phase of the trial, the contrast of the dioptic plaid dropped to zero for 250 ms, the aim being to preclude contrast summation between the dioptic gratings and the subsequently presented

dichoptic gratings (Hood & Finkelstein, 1986). After this brief blank period, the pair of dichoptic gratings was presented for a designated duration, with the onset of those gratings denoted by a "beep" sound. Following offset of the dichoptic gratings, the observer pressed one of three keys to indicate whether the percept at the time of stimulus offset corresponded to the +45° grating, the −45° grating or a mixture of the two (mixtures could consist either of the bits and pieces of the two gratings or the apparent superimposition of the two). Observers experienced no difficulty using these three categories, and they never experienced alternations in dominance during the dichoptic period because the longest exposure duration was only 700 ms.

3.4. Results

We first looked at performance on the catch trials (16% of the total number of trials) for which there were objectively correct responses. All of the observers responded correctly on 100% of these trials, verifying that they understood and followed the instructions.

Next we analyzed performance for those 84% of trials on which rival gratings were presented during the dichoptic phase. Consider first those trials on which no contrast increment was presented during the dioptic phase of the trial (i.e., trials on which the exogenous cue was not introduced). To derive baseline measures of initial dominance for these trials, we treated each of those trials as ones on which the cue *did* occur, only with the contrast increment being zero. In this way, we were able to calculate the percentage of trials on which the observer reported initial dominance of the "cued" orientation versus the "uncued" orientation, even though the cue itself was not physically present. Results for those baseline trials are shown in the right-hand panel of Fig. 2. As expected, responses were dis-

tributed evenly between the two alternative orientations, with mixture responses also being given on a substantial proportion of trials. These results, of course, are not surprising, for we have no reason to expect responses to be differentially distributed among the three possible categories on these "no-cue" trials.

Turning to the trials of interest (i.e., those on which the contrast increment cue was actually presented during the dioptic phase), we calculated the proportion of trials on which the initially dominant orientation corresponded to the orientation cued by a real contrast increment during the dioptic phase. Those results are shown in the left-hand panel of Fig. 2, for each of the four exposure durations used during the rival phase of the trial. Here it can be seen that the contrast increment during the dioptic phase clearly influenced initial dominance during the rivalry phase. Analysis of variance confirmed that the proportion of trials on which the cued orientation was initially dominant (58%, on average) was significantly ($F(1,4) = 12.73$, $p < .05$) greater than the proportion of trials on which the uncued orientation was initially dominant (13%). The main effect of exposure duration was not statistically significant nor was the interaction between exposure duration and cueing.

There were also trials involving cueing on which the observer reported 'mixed' dominance during the rivalry phase. The incidence of these 'mixed' trials was significantly lower when the dioptic phase included the exogenous attention cue (on average 29%), relative to trials when that cue was not present (44%; $F(1,4) = 28.43$, $p < .01$).

Shown in Fig. 3 are the results of Experiment 1b, where the timing of exogenous cue was manipulated. Again, observers were 100% correct on the catch trials. According to a two-way analysis of variance, the proportion of trials on which the cued orientation dominated initially was significantly higher than the proportion of trials on which the uncued orientation was dominant ($F(1,4) = 32.49$, $p < .01$); this merely replicates the main finding of Experiment 1a. More importantly, the interaction between trial category (cued dominant vs. uncued dominant) and the cue-lead time was statistically significant ($F(3,12) = 13.19$, $p < .01$), implying that exogenous attention was
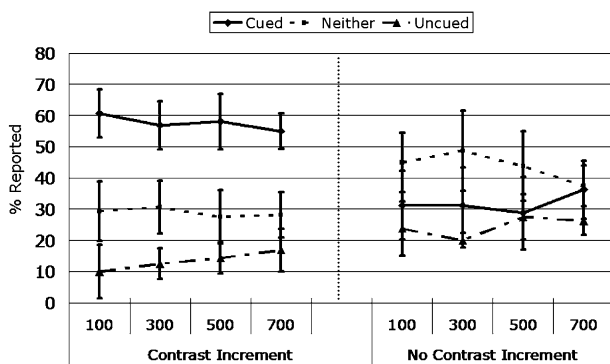

Fig. 2. The results of Experiment 1a (means and standard errors for five observers) for contrast-increment and no increment conditions. The *X* axis indicates the exposure duration of rival gratings presented during the dichoptic phase and the *Y* axis indicates percentage of trials on which observers reported initial dominance of the cued grating, the uncued grating, or a mixture of the two gratings ("neither"). For the contrast increment condition, the cued grating was the one whose contrast was briefly incremented 0.47 log-units during the dichoptic phase of the trial; for the no contrast increment condition, the cued grating was the one designated to receive the contrast increment but, in fact, was incremented not at all.
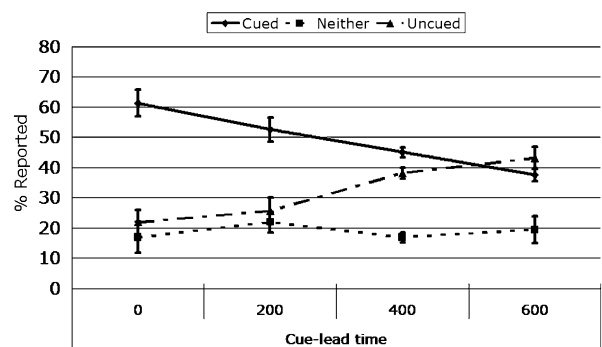

Fig. 3. The results of Experiment 1b (means and standard errors for five observers). The *X* axis indicates cue-lead time and the *Y* axis indicates the percentage of trials associated with the three response categories.

more effective when the contrast increment occurred very shortly before presentation of dichoptic gratings. To estimate the time at which the exogenous cue became effective, we performed a post hoc analysis on the difference between the cued and the uncued trials. This analysis revealed that the exogenous cue was effective only when the cue-lead time was either 200 ($p < .05$) or 0 ms ($p < .01$). This finding is consistent with previous results in which the time-course of exogenous attention was estimated using a visual search task (Nakayama & Mackeben, 1989) and a letter-matching task (Muller & Rabbit, 1989).

How do our findings compare to those of Mitchell et al. (2004)? In their study, the dioptic "cueing" phase lasted 1 s, with the cue itself (translational motion briefly replacing rotational motion) presented for 150 ms toward the end of the dioptic phase; they had no blank interval between the dioptic cueing period and the dichoptic test period (the duration of which ranged up to 1850 ms). At the briefest durations tested, their observers primarily experienced "mixtures" regardless of cueing; cueing (defined as the tendency for the cued optic flow field to be dominant initially in rivalry) reached full strength approximately 450 ms after the offset of the cue, implying that exogenous attention takes a brief period to be engaged (cf. Nakayama & Mackeben, 1989). Mitchell et al found little if any effect of exposure duration on cueing effectiveness (i.e., cueing remained strong for dichoptic exposure durations up to 1850 ms). We, too, found robust cueing only when rival targets were presented several hundred milliseconds after cue offset (Experiment 1b), and we observed that cueing is robust over a range of dichoptic exposure durations. Indeed, comparing our data to those of Mitchell et al. for comparable cue delay values, we find remarkable agreement in the strength of cueing. In our experiments we did not test cue delays less than 250 ms and did not, therefore, observe the high incidence of mixtures found by Mitchell and colleagues.

Both sets of results show, in other words, that attention directed exogenously to one of two stimuli causes that stimulus subsequently to dominate in rivalry. Our procedure rules out any contribution from differential adaptation during the dioptic, attention phase of each trial. If anything, the attended grating should produce greater adaptation (and hence be less likely to dominate in rivalry) because of the brief contrast increment to that grating. Moreover, our results go beyond those of Mitchell et al. by explicitly showing the time-course of exogenous attention's effect on initial selection in rivalry (Fig. 3).

In Experiment 2, we sought to learn whether initial selection in rivalry also could be influenced by endogenous attention directed at one of two stimuli.

4. Experiment 2: Endogenous attention

In Experiment 2, we used a feature tracking task to focus endogenous attention on the changing orientation of one of two dioptic stimuli that, subsequently, comprised dichoptic rival stimuli—with this task, sustained, willful attention is focused on that stimulus while both stimuli undergo equivalent changes in contour size and orientation during the cueing phase.

4.1. Stimuli

We used a display modeled after that described by Blaser, Pylyshyn, and Holcombe (2000) in their work on multi-feature tracking. In our modification of their display, both eyes viewed two superimposed gratings that formed a plaid. Five sampled frames of this dioptic stimulus are shown in Fig. 4. During the dioptic phase of each trial, both gratings underwent independent changes in their orientations and spatial frequencies for 5 s, with the following constraints. The initial orientations of the gratings in the first frame were $+45°$ ($\pm3°$) for one grating and $-45°$ ($\pm3°$) for the other. The initial spatial frequency of the first frame for each grating was the middle spatial frequency of the possible range (±0.1 cycles/deg). At the end of the 5 s dioptic tracking phase, the spatial frequency (4 cycles/deg) and orientations ($\pm45°$) of the two gratings were constrained to be the same as those subsequently appearing in the dichoptic phase.

During this 5-s period, orientation of the gratings could vary between $-74°$ and $+74°$, and the spatial frequency of the gratings could vary between 2.3 cycles/deg and 5.7 cycles/deg. Orientation changed at 1.3 angular deg/frame (13.33 ms) and spatial frequency changed at 0.03 cycles/deg/frame. Both orientation and spatial frequency tended to continue changing in a given direction, with a probability of direction reversal in either orientation or in spatial frequency being 10% unless either feature reached an upper or lower limit in which case a change inevitably occurred.

During the dichoptic/rival phase, orthogonally oriented gratings were presented separately to the two eyes, one grating oriented $+45°$ for one eye and the other oriented $-45°$ for the other eye. Exposure duration was either 250 or 500 ms. Again, catch trials were included, with the stimulus being either a single orientation presented to both eyes or the mock "mixed" grating presented to both eyes.

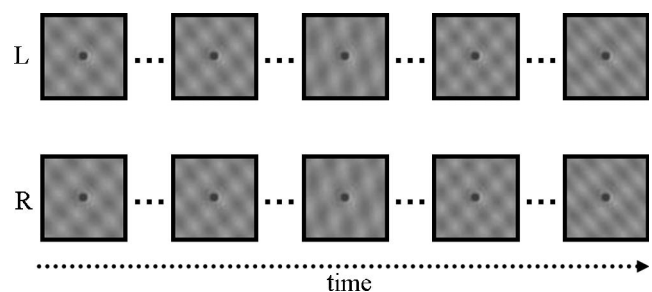Fig. 4. An example of the display used for the feature tracking task during the dioptic phase of each trial in Experiment 2. Shown here are five (nonconsecutive) frames showing changes in orientation and in spatial frequency. In the actual sequences, changes were smooth and less conspicuous.

The contrasts of all gratings in Experiment 2 were fixed at 13.4%.

4.2. Procedure

As in Experiment 1, each trial consisted of an initial dioptic phase during which attention was directed to one of two gratings (endogenously, this time), followed by a dioptic phase in which the two gratings were pitted against one another in rivalry. Each trial went as follows, First, prior to each trial, an on-screen instruction specified which one of the two plaid gratings the observer was to monitor during the 5-s dioptic phase; the instruction specified one of two orientations present in the plaid at the beginning of the dioptic exposure period. Following this instruction, the plaid itself appeared and remained stationary for 1 s to allow the observer to focus attention on the specified grating. Then, for the next 5 s, the gratings underwent changes in spatial frequency and orientation, and the observer's task was to monitor the changes in orientation of the attended grating. At the end of this 5 s period, both gratings remained stationary for a brief period of time sufficient for the observer to note whether the attended grating ended up oriented +45° or −45°. The changes in spatial frequency were irrelevant for performance of this task, but they did contribute to the difficulty of the task. Pilot work was used to establish a rate of orientation change that made the task sufficiently difficult to ensure that observers attended to the designated grating. The final phase of each trial comprised the brief presentation of the ±45° rival gratings to the two eyes (note, these two gratings corresponded in orientation and spatial frequency to the plaid components present at the end of the dioptic phase to prevent apparent motion from dioptic plaid to dichoptic gratings). At the end of each trial, the observer reported the resulting perceptual state (dominance of one or the other rival grating, or mixed dominance) and the orientation of the attentionally tracked grating at the end of the dioptic phase.

4.3. Results

Accuracy on the attentional tracking task (dioptic phase of the trials) averaged 87%, implying that the task could be performed but was sufficiently difficult to require sustained attention. Also, all observers were 100% correct on the various catch trials (dichoptic phase of the trials), implying that they were accurately reporting their percepts. The results summarizing initial dominance in rivalry are shown in Fig. 5; data were pooled for the two exposure durations because ANOVA revealed that results on these two conditions were not significantly different, nor was the interaction between exposure duration and trial type. We analyzed the proportion of cued, uncued and neither responses on trials when observers responded correctly on the orientation tracking task during the dioptic phase ("correct trials") and trials when observers were incorrect on the tracking task ("incorrect"). When correct in the
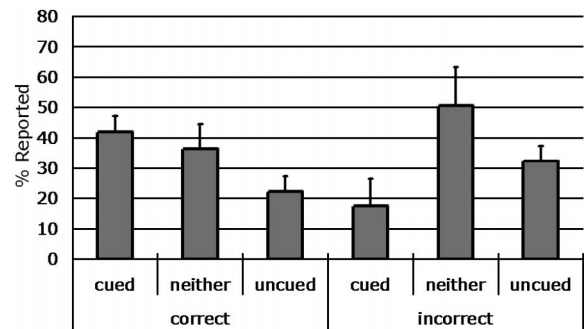

Fig. 5. The results of Experiment 2 (means and standard errors for five observers), where observers tracked changes in orientation of one of the dioptic gratings. The percentage of trials on which observers perceived mixtures ("neither"), the cued grating, and the uncued grating, plotted separately for trials on which observers were correct and were incorrect on the feature tracking task; results are pooled over two exposure durations (250 and 500 ms).

tracking task, observers reported initial dominance of the tracked grating more often than the not-tracked grating ($F(1,4) = 8.88$, $p < .05$). Thus, in other words, a grating at which endogenous attention was directed tends subsequently to dominate the initial selection of rivalry. When observers were incorrect in the tracking task, one might expect the opposite trend on the assumption that observers, for whatever reason, ended up tracking the wrong grating during the dioptic phase of the trial. Although the trend was indeed opposite for both dichoptic durations, main effect of type of trials did not reach statistical significance ($p = 0.09$). This result suggests that observers often just lost track of the designated grating rather than reliably tracking the wrong grating.

One might argue that sustained endogenous attention throughout the tracking period is unnecessary for the subsequent influence on rivalry dominance, with only the attentional state during the final, brief period of the dioptic phase influencing initial selection during the dichoptic phase. We are making no claims about how long endogenous attention must be engaged, but we are convinced that initial selection in rivalry was influenced by the success of attentional tracking during the dichoptic phase. Analysis of variance confirmed that the interaction between the type of trials and correctness of tracking performance was statistically significant ($F(1,4) = 10.29$, $p < .05$).

The magnitude of the effect of endogenous attention on initial dominance was weaker than was the effect of exogenous attention (compare cued vs. uncued results in Figs. 2 and 5). It is possible, of course, that we have underestimated attention's effect in the endogenous condition because that condition includes trials on which the observer simply guessed correctly on the "tracking" task but, in fact, did not have attention focused on that grating. There is no way to separate those trials from ones on which the observer's forced-choice judgment on the tracking task reflected genuine success on that task. There is no questioning, however, that endogenous attention is sufficiently robust to

influence initial selection in rivalry, without any involvement of physical stimulus changes or differential adaptation because of different exposure duration during dioptic stimulation.

5. Experiment 3: Estimating the effective strength of attention

How is it that attention, whether exogenous or endogenous, boosts the effective strength of a monocular target and thereby, enhances its likelihood of being the initially dominant stimulus during rivalry? Other work on visual attention implies that attention can increase the effective contrast of a visual pattern (Carrasco, Ling, & Read, 2004; Lu & Dosher, 1998). Moreover, it is well established that a higher contrast pattern predominates during rivalry (Levelt, 1965; Mueller & Blake, 1989), and in pilot work we have reliably found that a higher contrast rival pattern is much more likely to be the initially dominant stimulus at the onset of rivalry. Putting these observations together, we hypothesized that attention influences initial dominance by boosting the effective contrast of the attended pattern.

According to this hypothesis, we can make two predictions. First, attention directed to one of two gratings during the dioptic phase should *not* have an influence on rivalry selection if the two rival gratings are already very high in contrast. To test this prediction we replicated the endogenous attention task used in Experiment 2, this time using dioptic and dichoptic gratings all of 100% contrast. Among the six observers tested, the average % difference between cued and uncued trials was −4% (compare this to the average % difference of 20 in Experiment 2)—as predicted, attention is ineffective when the physical contrast of the rival gratings is already saturated.

Second, according to the contrast enhancement hypothesis, it should be possible to counteract attention's effect by reducing the actual contrast of the rival grating receiving attention during the dioptic phase, thereby re-establishing stimulus conditions wherein initial predominance is equally distributed between the two alternatives. Indeed, by adaptively varying the actual contrast of a previously attended pattern, it should be possible to estimate the effective boost in contrast by finding the contrast at which initial predominance is equal for the two competing patterns. This was the purpose of this last experiment.

5.1. Stimuli

Experiment 3a utilized the same stimuli as those used in Experiment 1 and Experiment 3b used the same stimuli as those used in Experiment 2.

5.2. Design

Experiment 3a employed the exogenous attention manipulation to cue attention, i.e., a contrast increment to one of two plaid components; Experiment 3b used the

endogenous attention manipulation to cue attention, i.e., observers tracked the changing orientation of one of two plaid components. During the diochoptic phase of each trial, we used an adaptive staircase procedure to vary the contrast of the "cued" grating from trial to trial, the aim being to estimate the contrast at which initial selection of that grating was equivalent to the likelihood of selecting the uncued grating. Thus, following trials on which the observer reported initial dominance of the "cued" rival grating, the contrast of that grating was reduced on the next trial; following trials on which the uncued grating's orientation dominated during the dichoptic rival presentation, contrast was increased on the next trial. Following trials on which the observer reported mixed dominance, the contrast of the cued grating remained the same. Two randomly interleaved staircases were administered concurrently, one starting with an initial contrast of 21% for the cued grating and the other starting at an initial contrast of 7.8% for the cued grating. The contrast of the other, uncued grating remained constant at 13.4%. We also administered two additional staircases with the same initial contrasts without attentional modulation, in order to measure baseline point of subjective equality. Contrast was changed from trial to trial in steps of 2%, and the staircase was terminated after 15 reversals. We computed the average of the contrast associated with the last 4 reversals for the two independent staircases. This value provides the estimate of the grating contrast necessary to produce balanced initial selection between the cued and the uncued rival gratings. Catch trials were not included for these experiments.

5.3. Results

Results are shown in Fig. 6. For every observer, the contrast of the cued grating required to balance selection was lower than the (fixed) contrast of the uncued grating, for both exogenous and endogenous conditions. On average, the contrast of an exogenously cued grating had to be 8.5% in order for its potency to be reduced to the point
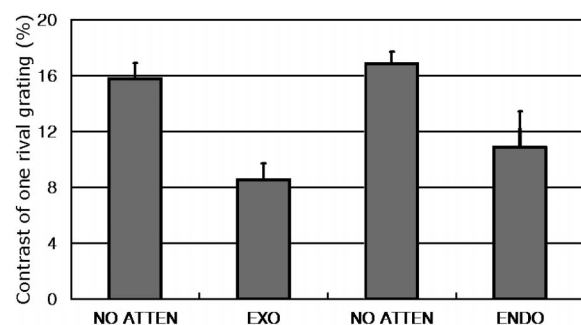

Fig. 6. The results of Experiment 3 (means and standard errors). *Y* axis plots the contrast of one rival grating necessary for that grating to be initially selected in rivalry 50% of the time. In the NO ATTEN condition, attention was not directed to either grating during the dioptic phase; in the EXO condition (four observers) and the ENDO condition (three observers), attention was directed exogenously or endogenously, respectively, to one of the dioptic gratings.

where that grating was no more likely than the other, 13.4% contrast grating to achieve initial dominance. For the endogenously cued grating, contrast had to be 10.8% to achieve equi-probably initial dominance. For the control conditions where attention was not directed to either grating, equi-probably dominance was achieved when the grating whose contrast was varied by the staircase averaged 16%. This value is slightly higher than 13.4%, the contrast of the uncued grating, which may be because we varied contrast in linear, not log, steps. In any event, this slight bias is in the opposite direction of the values needed to offset the modulatory effect of attention.

Thus, we find that attention's influence on initial dominance in rivalry can be nullified by reducing the physical contrast of that cued grating, by an amount in the neighborhood of 0.3 log-units. While these results do not prove that attention really does boost the effective contrast of a pattern, they are consistent with other psychophysical evidence implying that attention alters the effective contrast of a visual stimulus (Carrasco et al., 2004). Moreover, our results square nicely with results from single cell recordings from visual area MT (Martinez-Trujillo & Treue, 2002) and V4 (Reynolds & Chelazzi, 2004; Reynolds & Desimone, 2003) showing that the boost in neural response associated with attention can be mimicked by a 50% increase in actual contrast (a value in excellent agreement with our finding).

6. Discussion

As we knew from the earlier work by Ooi and He (1999) and Mitchell et al. (2004), exogenous attention can influence initial dominance in binocular rivalry. The present results confirm this observation but, more importantly, extend our understanding of attention's influence on rivalry selection in three ways. First, our results show exogenous attention is effective only when the transient cue designed to capture attention occurs within about a 1/2 s period prior to the onset of the dichoptic rival targets. Second, our results show that initial selection in rivalry is also influenced by *endogenous* attention. Third, attention's influence on initial rivalry dominance can be counteracted by reductions in the physical contrast of the rival pattern toward which attention had been directed.

Attention's ability to bias initial selection when stimuli compete for perceptual dominance is not really surprising—after all, attention has ubiquitous influences throughout all aspects of vision (Pashler, 1999). Indeed, attention is commonly characterized as a mechanism whose prime purpose is to select, or augment, one stimulus from among many that together may tax limited processing resources. Considered in this light, attention's influence on binocular rivalry would seem to represent a paradigmatic instance of the operation of selection, just as Helmholtz proposed 150 years ago (Helmholtz, 1925). What Helmholtz did not address—but what contemporary results suggest—is the means by which attention may be influencing selection during rivalry. Specifically, our results dovetail nicely with the

emerging view that attention serves to modulate the strength of one stimulus relative to other, competing stimuli (Reynolds & Chelazzi, 2004). How does this operate in the case of binocular rivalry?

We know that a higher contrast stimulus tends to dominate a lower contrast stimulus, meaning that the higher contrast pattern dominates perception for a larger percentage of the total viewing time (Levelt, 1965; Mueller & Blake, 1989). This influence of contrast is particularly strong at the onset of rivalry: a stronger contrast rival target will nearly always be the target seen initially at the onset of dichoptic stimulation (results from our pilot study). From the work of Carrasco et al. (2004), we know that attention directed to a grating increases that grating's apparent contrast. The magnitude of this boost in contrast varies between 30% and 70%, depending on the actual contrast of the attended grating; the effective boost we measured in Experiment 3 was 47%. Moreover, Carrasco et al. (2004) found that this attentional boost in apparent contrast was short-lived, dissipating within 500 ms of the offset of the attentional cue. In our study, the interval between offset of the dioptic (attentional) display and the onset of the dichoptic (rivalry) display was always 250 ms (a value selected to preclude contrast summation between dioptic and dichoptic gratings). We also found no exogenous attention effect when the exogenous cue preceded the dichoptic stimuli more than 450 ms. Putting Carrasco's results together with the known influence of contrast disparity on rivalry, we are drawn to the conclusion that attention influences initial selection by increasing the effective contrast of an attended pattern. Certainly the results from our Experiments 3a and 3b and are consistent with this conclusion, for we showed that attention's effect can be counteracted by reducing the actual contrast of the rival target toward which attention was drawn a fraction of a second earlier. Finally, we showed the failure of attention to influence selection when rival gratings had high contrast.

This conclusion moreover is consistent with the results from single cell recordings. In a recent review of that neurophysiological literature, Reynolds and Chelazzi (2004) concluded that attention to a stimulus within a neuron's receptive field produces a boost in neural response equivalent to that associated with a 51% increase in contrast. This value compares quite favorably with the 47% estimate found in our Experiment 3. It should be acknowledged, however, that the neurophysiological studies typically manipulated attention by having a monkey attend either to a stimulus in the recorded neuron's receptive field or to a stimulus located outside that receptive field. In our studies, however, the attended stimulus occupied the same location as the unattended stimulus.

We, unlike Mitchell et al. (2004), also studied the influence of endogenous attention on initial selection during rivalry. Although robust, the effect of endogenous attention appears to be weaker than that of exogenous attention. This may be attributable, in part, to the necessary procedural differences between these two conditions. Exogenous attention

was directed to one of two patterns by introduction of a contrast increment to that pattern, a strategy that unambiguously earmarks one of the two patterns as the "attended" stimulus. Endogenous attention, on the other hand, was tied to the observer's successfully tracking one of two changing patterns for a period of time, a difficult task that was bound to produce mistakes (including mistakes on trials where the observer nonetheless guessed correctly).

What are the implications of our results for theories of binocular rivalry? For several decades, two competing views of rivalry were pitted against each other, one being an "early" eye-based account (e.g., Blake, 1989; Sugie, 1982) and the other a "late" stimulus-based account (e.g., Logothetis, Leopold, & Sheinberg, 1996; Walker, 1978). Recently, however, these competing views have been amalgamated into a hybrid model in which rivalry is viewed as the culmination of a cascade of distributed neural events (Blake & Logothetis, 2002). On this hybrid model, different aspects of rivalry are distinguished from one another. Thus, the neural events triggering rivalry and initial selection may not be identical to those underlying rivalry dynamics, and the neural circuitry mediating suppression of one eye's stimulus may differ from the constellation of neural circuits promoting dominance of the other eye's stimulus. At the same time, there is an emerging view that attention itself can modulate neural activity at multiple stages of the visual hierarchy (Kastner, 2004; Liu, Pestilli, & Carrasco, 2005; Reynolds & Chelazzi, 2004). Given these emerging conceptualizations of rivalry and attention, it could be an overstatement to assert, based on attention's influence on rivalry, that binocular rivalry involves competition between high-level stimulus representations. It is entirely feasible that attention could modulate different aspects of rivalry to varying degrees. Thus, attention may strongly influence the initially dominant stimulus in rivalry (Ooi & He, 1999; Mitchell et al., 2004; the present results) yet exert a weaker influence on the dynamics of rivalry (Chong et al., in press; Meng & Tong, 2004; van Ee et al., 2005). Similarly, attention may augment global, contextual features that enhance the dominance of a stimulus (e.g., Kovacs, Papathomas, Yang, & Feher, 1996; Sobel & Blake, 2002; Silver & Logothetis, 2004) while, at the same time, having essentially no influence on contextual strengthening during suppression phases (Lee & Blake, 2004; Sobel & Blake, 2002).

So, in conclusion, the present results, together with those of Ooi and He and of Mitchell et al, point to a robust effect of attention on initial selection. Moreover, this influence occurs regardless whether attention is directed to a stimulus by exogenous or endogenous means. Whether attention's potency can be applied with equal force to other aspects of rivalry is a question that deserves further consideration.

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