The following full text is a publisher's version.

For additional information about this publication click this link.
http://hdl.handle.net/2066/135884

Please be advised that this information was generated on 2019-12-26 and may be subject to change.
Eye dominance alternations in binocular rivalry do not require visual awareness

Artem Platonov

Radboud University Medical Centre Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Dept. of Cognitive Neuroscience, section Biophysics, Nijmegen, The Netherlands

Jeroen Goossens

Radboud University Medical Centre Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Dept. of Cognitive Neuroscience, section Biophysics, Nijmegen, The Netherlands

Binocular rivalry provides a valuable means to study how sensory processing gives rise to subjective experiences because it involves a changing percept without any change in the visual stimulus. An important question, however, is whether visual awareness is necessary for binocular rivalry to emerge. To address this question, we presented conflicting random dot motion stimuli in the two eyes at luminance contrasts around perceptual threshold. We asked subjects to report continuously, via button presses, if they noticed any kind of motion in the display (be it coherent or not) and indicate which direction of motion they thought was dominant at any given instant even if they were unaware of any motion in the display. We biased the competition between the two dichoptic stimuli by changing the motion coherence in one eye while keeping it fixed in the other to test if this induced predictable changes in rivalry dynamics. We also probed the strength of the interocular suppression. Our data show that binocular rivalry continues even if subjects claim complete absence of visual motion awareness. This remarkable dissociation between visually guided behavior and visual awareness resembles the dissociation seen in other phenomena, such as blindsight and visual masking. Fluctuations in awareness that did occur were temporally linked to the dominance switches in a manner that is consistent with adaptation reciprocal-inhibition models of binocular rivalry.

Introduction

Binocular rivalry is a phenomenon that occurs when our eyes receive stereo-incompatible inputs at the same retinal location. This leads to perceptual alternations between the two images even though both stimuli are constantly present. The fact that our percept changes without any change in the visual stimulus (Blake & Logothetis, 2002; Kim & Blake, 2005; Rees, Kreiman, & Koch, 2002; Tong, 2003) advocated the use of binocular rivalry to study the neural basis of conscious visual perception (Leopold & Logothetis, 1996) and qualified it as a “window on consciousness” (Logothetis, 1999). It has been shown, however, that the suppression of one eye’s image corresponds only to a partial loss of contrast sensitivity to probe stimuli in that eye (Blake & Fox, 1974; Fox & Check, 1968, 1972; Nguyen, Freeman, & Alais, 2003; Norman, Norman, & Bilotta, 2000), indicating that those inputs are still processed by the brain. This notion is further supported by the fact that a suppressed stimulus can still affect the currently dominant percept by changing its perceived orientation (Pearson & Clifford, 2005), direction of motion (Andrews & Blakemore, 2002), luminance (Carlson & He, 2000), and color (Carney, Shadlen, & Switkes, 1987; Holmes, Hancock, & Andrews, 2006; Hong & Shevell, 2009) and still provides disparity cues enabling stereoscopic depth perception (Andrews & Holmes, 2011; Su, He, & Ooi, 2009). Moreover, stimulus-specific activation in striate and extrastriate cortical areas does not necessarily result in awareness of the underlying stimulus (Haynes & Rees, 2005; He, Cavanagh, & Intriligator, 1996; Moutoussis & Zeki, 2006). Thus, it is possible that binocular rivalry occurs even in the absence of visual awareness. We tested this possibility in two experiments in which we studied dominance and suppression of rivalrous random dot motion stimuli whose luminance contrasts were set around perceptual threshold.
A key feature of binocular rivalry is that decreasing the “stimulus strength” in one eye primarily increases the mean dominance duration of the other eye while the mean dominance duration of the eye in which the stimulus strength is manipulated remains almost unaffected (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Levelt, 1966). This relationship, known as Levelt’s second proposition (L2, Levelt, 1965), may seem counterintuitive at first glance but is easily explained in terms of reciprocal inhibition in which a given stimulus does not generate an isolated response but one linked to the response generated by another competing stimulus (Blake, 1989; Freeman, 2005; Lehky, 1988; Noest, van Ee, Nijs, & van Wezel, 2007; Platonov & Goossens, 2013; Wilson, 2003). Most previous studies have varied stimulus contrast to investigate the influence of “stimulus strength” on the dynamics of binocular rivalry alternations (e.g., Brascamp et al., 2006; Fox & Rasche, 1969; Mueller & Blake, 1989). We have recently shown, however, that changes in motion coherence are equally effective (Platonov & Goossens, 2013). We also noticed, in that study, that subjects were no longer aware of any motion in the display when we presented rivalrous motion stimuli at contrast levels for which they could still easily discern (>75% correct) the direction of motion in unambiguous motion patterns. We thus reasoned that it should be possible to manipulate visual awareness by changing the luminance contrast around the subjects’ motion discrimination threshold and then test L2 under these different conditions by lowering the proportion of coherently moving dots in one eye while keeping it fixed at 100% in the other and asking our subjects to indicate which direction of motion they thought was dominant at any given instant even if they were unaware of any motion in the display. To assess whether or not the subjects were aware of visual motion at the time of these decisions, we also asked them to indicate continuously whether or not they noticed any kind of motion in the display. In this way, we could also study the temporal relationship between state changes in awareness and dominance switches. In the second experiment, we used a probe detection paradigm (Fox & Check, 1968; Stuit, Cass, Paffen, & Alais, 2009) to test if the dominance alternations reported in the first experiment indeed resulted from eye dominance alternations.

Materials and methods

Subjects

Seven healthy human subjects with (corrected to) normal visual acuity and normal stereovision participated. They were naive to the purpose of the experiments. All gave informed consent for participa-

tion. The experiments were approved by the Radboud University Nijmegen Medical Centre.

Setup

Subjects were seated in front of a liquid crystal display (Dell, 2007WFPb; resolution 1680 × 1050 pixels, 60-Hz refresh rate) in an otherwise dark room with their head supported by a headrest. The visual stimuli were generated by a personal computer equipped with an openGL graphics card using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) for Matlab (The MathWorks, Inc., Natick, MA). The images were presented separately to the left and right eyes by means of a front-mirror stereoscope (HyperView, Berezin; viewing distance 67 cm). The display was calibrated with a precision Minolta Luminance Meter LS-100.

Visual stimuli

The dichoptic stimuli consisted of two independently generated random dot kinematograms (RDKs) each containing 533 white dots (2 × 2 pixels, 0.05°) that moved against a gray background. Signal dots were refreshed asynchronously. At the beginning of its lifetime, each dot started at a random location within the circular aperture (4° radius) and then moved leftward or rightward at 4.2°/s for four frames (66.7 ms). Dots that moved outside the aperture were wrapped to the opposite side of the aperture. Noise dots—if present—moved to a new random location within the aperture on each subsequent frame. We manipulated the luminance of the dots as well as the percentage of signal dots. The background luminance was always 15.43 cd/m².

Motion discrimination threshold

For each participant (n = 7), we first determined the contrast threshold for his/her monocular motion direction–discrimination performance using a two-alternative forced-choice task (2AFC). This task required the subject to discriminate between leftward and rightward monocular motion stimuli that contained 100% coherently moving dots. Each trial started with a button press, followed by the presentation of a central fixation point, which the subject had to fixate for the remainder of the trial. Subsequently, a visual motion stimulus was presented in either the left or the right eye for 0.5 s. At the end of each stimulus presentation, the subject had to indicate the perceived direction of motion, guessing if necessary. In each trial, the luminance of all dots was set to one of six possible levels between 15.43 cd/m² and 18.69 cd/m², corre-
Experiment 1: Dominance alternations

Paradigm

In the first experiment, we manipulated the luminance contrast of rivalrous motion stimuli (Figure 1A) corresponding to contrasts in the range of 0%–10% Michelson. The background luminance (15.43 cd/m²) was the same in both eyes. Thresholds (75% correct; averaged across left and right eyes) were around 5% Michelson (also see Platonov & Goossens, 2013).

Figure 1. Motion rivalry paradigm with contrast manipulation to influence visual motion awareness. (A) Subjects were dichoptically presented with a central fixation point (+) and two random dot motion patterns in which the dots moved coherently in opposite directions. Arrows indicate the direction of motion of the moving signal dots. Bullets represent noise dots, which appeared at a random location within the aperture in each frame. The percentage of coherently moving dots was kept fixed at 100% in one eye (here the left eye) and manipulated between 30% and 90% in the other eye (here the right eye). Motion directions and coherence manipulations were randomly swapped between the two eyes across trials. We tested three contrast conditions (approximately, 4.9%, 6.3%, and 7.8% Michelson in both eyes) close to the subjects’ monocular motion direction–discrimination threshold (≈5% Michelson). (B) Example of changes in visual awareness and motion-direction dominance in one of our subjects over a series of trials (different rows) in the medium-contrast condition. Subjects reported continuously if they were aware of any visual motion in the display (gray), regardless of its appearance, and had to indicate whether the direction of coherent motion was predominantly to the left (green) or to the right (red), guessing if necessary. Remarkably, alternations between dominance of the leftward and rightward motion direction did not require awareness of visual motion. (C) Percentage of total viewing time during which subjects indicated awareness of any visual motion (be it coherent or not) in the low- (light gray), medium- (gray), and high- (black) contrast conditions increased with increasing contrast. At the lowest contrast (≈4.9% Michelson), subjects were almost always unaware of any visual motion in the stimulus. Coherence did not affect the percentage of visual motion awareness. Data are averaged across subjects (n = 5). Error bars indicate ±1 SEM.
m² above (medium contrast, ~6.3% Michelson), or 0.75 cd/m² above (high contrast, ~7.8% Michelson) the subject’s monocular motion direction–discrimination threshold; 0.25 cd/m² was the smallest practical change in luminance permitted by our equipment. This approach ensured that the contrast manipulation produced robust changes in visual awareness (see results, Figure 1B) while the monocular stimuli themselves had sufficient contrast to support motion-direction discrimination well above chance. A trial began with a 0.2° central fixation cross. Subsequently, RDKs with horizontal motion in the two opposite directions were presented to the left and right eyes for 60 s. Subjects were instructed to fixate the fixation cross and perform a motion-detection task by pressing and holding the middle button as long as they were able to perceive any visual motion, regardless of its appearance. In addition, they were asked to discriminate between the two directions of motion, even if they were unable to discern any visual motion whatsoever, by pressing and holding one of the two mouse buttons as long as either one of the motion directions was thought to be dominant, guessing if necessary.

Motion directions (temporal-to-nasal or nasal-to-temporal) and eye of manipulation were counterbalanced across trials. To avoid big luminance changes between trials, they were organized in randomized blocks of either low and medium contrast stimuli or medium and high contrast stimuli. All subjects (n = 5) accomplished six low/medium blocks and four medium/high blocks. This resulted in 12 trials per coherence/contrast condition after pooling the data across eyes.

We also ran two control experiments with two additional subjects, in which we interleaved low-contrast stimuli with catch trials (see Supplementary Appendix). In the first of those experiments, the catch trials contained no stimulus other than the fixation cross. In the second one, the low-contrast RDKs presented in the catch trials only contained dynamic noise.

Data analysis

Dominance durations and predominance

To analyze the data, we marked all phases of motion awareness indicated by the middle button presses and calculated the percentage of total viewing time during which subjects indicated awareness of visual motion. We also marked all phases of leftward and rightward motion-direction dominance based on the left and right button presses. For each trial, we then calculated the mean dominance duration of each motion direction as well as its predominance; predominance is defined as the percentage of the total viewing time during which a given motion direction was dominant. Truncated dominance states at the end of a trial were included in the predominance measure. For computing the mean dominance duration, we included truncated states that encompassed more than 85% of the total trial duration. The resulting values were then averaged across trials, pooling motion-direction dominance according to the eye receiving that stimulus (i.e., the ipsilateral and contralateral eye). We compared the results across conditions using repeated measures analysis of variance (ANOVA). We also used analysis of covariance (ANCOVA) to fit linear regression lines to the data and applied Student’s t-tests on the resulting fit parameters to evaluate changes in the response curves. Test results reported in the text always refer to the group statistics.

For the low-contrast condition, we also calculated predominance and mean dominance durations from the epochs containing no episodes of visual awareness. For the medium-contrast condition, we split all dominance durations into “high awareness” and “low awareness” groups. To this end, we first computed, for each dominance epoch, the percentage of time during which the subject indicated being aware of visual motion, i.e., the awareness fraction. We then calculated the distribution of awareness fractions across all dominance epochs and assigned all dominance epochs with an awareness fraction above the 50th percentile to the high-awareness data set and those with awareness fractions below the 50th percentile to the low-awareness data set. These filtered data sets were subsequently analyzed in the same fashion as the unfiltered ones.

Cross-correlations

The temporal relationship between changes in awareness and dominance was investigated with cross-correlation analyses in the time and phase domain. We first computed cross-correlograms representing the average occurrence density of awareness onset and offset (in counts per second) as a function of time (in seconds) relative to the dominance switches (Figure 4A). These cross-correlograms were generated with a temporal resolution of 60 bins/s and convolved with a Gaussian smoothing kernel (width σ = 0.2 s). To test whether the resulting peaks were statistically significant in individual subjects, we first corrected the raw cross-correlograms with the so-called shift predictor (a measure of the correlation that can be expected under the null hypothesis that there is no physical relationship between the two different events; see Aertsen, Gerstein, Habib, & Palm, 1989; Gerstein & Kiang, 1960) and then applied the bootstrap excursion (BE) test developed by Ventura, Cai, and Kass (2005). See Kalisvaart and Goossens (2013) for a more detailed description of this procedure. We then tested whether awareness exhibits phase locking with respect to the dominance alternation cycle. Toward that end, we computed the
awareness probability as a function of phase in the two subsequent dominance intervals (Figure 4B). Phase refers to the normalized timing in these two intervals. By convention, we normalized the relative timing during each individual dominance interval of motion stimuli in the manipulated ipsilateral eye between −1 and 0 in such a way that −1 and 0 correspond with its onset and offset, respectively. The relative timing during dominance intervals of motion stimuli in the fixed contralateral eye was normalized between 0 and 1 so that their onsets and offsets correspond with phase values of 0 and 1, respectively. The probability curves were computed with a resolution of 36 bins per dominance state (so 72 bins in total across the full alternation cycle).

Figure 2. Changes in motion-direction dominance carry the signature of binocular rivalry. Predominance (A) and mean dominance durations (B) of the motion direction presented in the fixed (solid) and manipulated (dashed) eye in the low- (light gray), medium- (gray), and high- (black) contrast conditions as a function of motion coherence in the manipulated eye. Note that decreasing the motion coherence in one eye produced a robust increase in predominance and mean dominance durations of the motion direction presented in the contralateral fixed eye. After removing, from the low-contrast data, all dominance epochs with episodes of visual motion awareness, there were still significant changes in predominance (C) and mean dominance durations (D) as a function of ipsilateral motion coherence. As for the unfiltered data, these changes complied with L2 (Levelt, 1965). Data are averaged across subjects (n = 5). Error bars indicate ±1 SEM.

Finally, we examined whether the occurrence of dominance switches was phase locked to the changes in awareness (Figure 5). Toward that end, we determined the average switch counts as a function of their normalized timing relative to the awareness onsets (at phase 0) and offsets (at phase −1 and +1). These occurrence density curves were computed with a resolution of 36 phase bins per awareness state (72 bins in total across the full unaware-aware cycle) and convolved with a circular Gaussian smoothing kernel (width σ = 2 bins). We used ANOVA to test whether phase locking was statistically significant and possibly influenced by our stimulus manipulation.

Results

As outlined above, we presented rivalrous motion stimuli at different contrast levels close to the subjects’
motion awareness, ANOVA main effect: no significant effect on the average level of visual awareness, and we varied the percentage of coherently moving dots in one eye while keeping it fixed at 100% in the other to test if these monocular changes in motion coherence systematically biased the competition between the two motion patterns (Figure 1A).

We asked the subjects to perform a motion-detection task in which they had to indicate continuously if they noticed any visual motion in the display, be it coherent motion, dynamic noise, or any other kind of visual motion. We also asked them to perform a 2AFC task in which they had to discriminate continuously which direction of motion was dominant at any given moment, guessing if necessary. Figure 1B illustrates the responses of one subject (S1) in the medium-contrast condition when the proportion of coherently moving dots in the manipulated eye was 90%. Note that the subject reported switches in dominance of the leftward (green) and rightward (red) motion direction regardless of whether she was aware (gray) or unaware of any motion in the stimulus patch.

Figure 1C quantifies the average percentage of total viewing time during which the subjects indicated being aware of any visual motion in the display for the high- (black), medium- (gray), and low- (black) contrast conditions. Analysis of variance (ANOVA) indicated a significant main effect of contrast on this measure of visual awareness, \( F(2, 788) = 90.444.6, p < 0.001 \); it decreased from nearly 98% in the high-contrast condition to never reaching 15% in the low-contrast condition. Motion coherence, on the other hand, had no significant effect on the average level of visual motion awareness, ANOVA main effect: \( F(3, 788) = 0.68, p > 0.5 \); contrast x coherence interaction: \( F(6, 788) = 0.52, p > 0.75 \). The percentage of false alarms in these subjective awareness reports proved to be negligibly small as subjects almost never reported motion awareness during catch trials in which no stimulus was presented (control experiment in two naïve subjects; Supplementary Appendix, Figure A1).

Levett's second proposition

Given that our subjects were often unaware of motion in the stimuli, especially in the lowest contrast condition, it is not obvious that a particular motion-direction judgment can be linked to dominance of the eye receiving that motion stimulus. Indeed, on de-briefing, our subjects reported that they were very uncertain about their motion-direction judgments. It is possible therefore that they were just guessing randomly instead of reporting true alternations in eye dominance. If this were the case, however, systematic manipulation of the motion coherence in one eye should not produce any systematic difference in reported dominance of the two directions of motion. By contrast, if eye dominance alternations continue in the absence of visual awareness and subjects consistently use information from the dominant eye to perform the discrimination task, their motion-direction judgments should, on average, correlate with the direction and coherence of the manipulated motion pattern. More specifically, in this case, one would expect an increasing difference between mean dominance durations of the two motion directions as a function of decreasing coherence in the manipulated eye. In fact, as outlined in the Introduction, one would expect these changes to obey L2 because it is one of the hallmarks of binocular rivalry. Therefore, if binocular rivalry persists in the absence of visual awareness, decreasing the motion coherence in one eye should mainly increase dominance durations of the motion direction presented in the other eye and, consequently, boost predominance of the motion direction presented in that eye as we previously observed for high-contrast motion stimuli (Platonov & Goossens, 2013).

The left-hand panels in Figure 2 show the average predominance (Figure 2A) and mean dominance durations (Figure 2B) of motion direction presented in the ipsilateral and contralateral eyes under the low- (light gray), medium- (gray) and high- (black) contrast conditions. The data are plotted as a function of decreasing coherence in the manipulated eye. Note that changing the motion coherence in one eye led to significantly different changes in predominance (Figure 2A), ANOVA, eye x coherence interaction, \( F(3, 1576) = 124.11, p < 0.001 \), and mean dominance durations (Figure 2B), ANOVA, eye x coherence interaction, \( F(3, 1576) = 64.24, p < 0.001 \), of the...
motion direction presented to that eye and the contralateral eye. As coherence in one eye decreased, both predominance and mean dominance durations of motion direction in the other eye’s pattern increased systematically from near symmetric dominance of the two stimuli to almost exclusive dominance of motion direction presented in the contralateral fixed eye. This effect was consistently observed in all our subjects. By contrast, there were no significant biases toward one or the other motion direction if the signal dots in both eyes were replaced with noise or if there was no stimulus at all (see Supplementary Appendix, Figure A2).

We used analysis of covariance (ANCOVA) to quantify the characteristic response patterns shown in Figure 2. The results demonstrated that decreasing the coherence in one eye’s motion pattern indeed caused a significant increase in dominance of the other eye’s motion pattern. This is reflected by the negative slopes for the low- (Figure 2B, light gray solid curve), slope $\alpha = -7.12 \pm 0.62, t(2) = -7.29, p \ll 0.001$; medium- (Figure 2B, gray solid curve), slope $\alpha = -6.72 \pm 0.47, t(2) = -8.67, p \ll 0.01$; and high- (Figure 2B, black solid curve), slope $\alpha = -10.60 \pm 0.72, t(2) = -8.12, p \ll 0.01$, contrast conditions alike. Moreover, as predicted by L2, the increase in mean dominance durations of the fixed eye’s motion pattern was, on average, more than four times steeper than the concomitant decrease in mean dominance durations of the motion direction presented in the manipulated eye. This significant difference in slope was observed for the low-, $\alpha = 1.90 \pm 0.62, t(2) = 7.29, p \ll 0.001$; medium-, $\alpha = 1.37 \pm 0.47, t(2) = 8.67, p \ll 0.001$; and high-, $\alpha = 1.14 \pm 0.72, t(2) = 8.12, p \ll 0.001$, contrast conditions alike.

The compliance with L2 even in the lowest contrast condition is quite remarkable. But due to the presence

Figure 4. Temporal relationship between dominance switches and changes in awareness. (A) Cross-correlation between dominance switches and awareness onsets ($A_1$) and offsets ($A_2$) on an absolute time scale. Data for the low- (light gray), medium- (gray), and high- (black) contrast conditions are taken from the 90% coherence condition and averaged across subjects ($n = 5$). (B) Awareness probabilities in the low- (light gray), medium- (gray), and high- (black) contrast conditions plotted as a function of phase in the dominance alternation cycle for the 30% ($B_1$), 50% ($B_2$), 70% ($B_3$), and 90% ($B_4$) coherence conditions. Negative and positive phase values correspond with normalized dominance time of the motion direction presented in the ipsilateral and contralateral eyes, respectively. Data are averaged across subjects ($n = 5$). Error bars indicate $\pm 1$ SEM.
of brief motion awareness epochs, it is not immediately clear whether L2 still holds when the stimuli did not reach the threshold for visual awareness. To test for this, we also quantified the mean durations of dominance epochs that contained no episodes of visual motion awareness. The right-hand panels in Figure 2 plot the resulting predominance (Figure 2C) and mean dominance durations (Figure 2D) of the two eyes’ motion patterns across all unaware dominance epochs under the low contrast condition. Analysis of this cleaned-up data set also shows that decreasing the coherence in one eye led to significantly different changes in predominance (Figure 2C), ANCOVA, eye × coherence interaction, $F(1, 476) = 34.42, p \ll 0.001$, and mean dominance durations (Figure 2D), ANCOVA, eye × coherence interaction, $F(1, 476) = 25.07, p \ll 0.001$, of the motion direction in the manipulated and fixed eyes. Moreover, the decrease in mean dominance durations of the fixed eye’s motion pattern with decreasing motion coherence in the manipulated eye, $(z = -4.66 \pm 0.62, t(2) = 5.01, p \ll 0.001)$, was, on average, more than two times steeper than the concomitant increase in dominance of the motion direction in the manipulated eye, $(z = 1.60 \pm 0.62, t(2) = 7.29, p \ll 0.001)$. Thus, our results demonstrate that monocular changes in motion coherence systematically biased the durations of the motion direction–dominance states in accordance with L2 even if subjects were unaware of any visual motion in the display. This strongly suggests that binocular motion rivalry proceeds in the absence of visual awareness, but it does not mean that visual awareness (or attention) has no influence on the rivalry dynamics or that their time courses are independent.

**Influence of awareness level**

Our ANCOVA indicated that the effect of ipsilateral motion coherence on predominance, $t(2) = -13.47, p \ll 0.001$, and mean dominance durations, $t(2) = -11.86, p \ll 0.001$, of the other motion pattern was significantly different between the three contrast conditions, but it is difficult to dissociate whether this interaction effect was due to changes in stimulus contrast or due to the
concomitant changes in visual awareness (c.f., Figure 1C). Interestingly, however, for the low-contrast condition, the changes in mean dominance duration of motion direction in the contralateral eye were steeper when data were pooled across aware and unaware states (Figure 2B, light gray solid curve) compared with the data from unaware states only (Figure 2D). This suggests that the level of visual awareness itself does influence the rivalry dynamics.

To further test if the average level of visual awareness influenced the rivalry dynamics, we analyzed the mean dominance durations obtained in the medium contrast condition by splitting them into high-awareness and low-awareness groups (see data analysis). We used the data from the medium-contrast condition because this condition yielded a relatively large variation in the awareness fraction across dominance intervals due to the fact that the subjects were, on average, aware of visual motion for about 40% of the viewing time (c.f. Figure 2). Figure 3 plots the resulting mean dominance durations of motion direction in the manipulated (dashed) and fixed (solid) eyes for the low-(gray) and high- (black) awareness data. Intercepts of the regression lines for the high-awareness data were significantly higher for motion patterns in the fixed eye, ANCOVA, t(1) = 4.54, p < 0.001, compared with the low-awareness data. Moreover, the difference in slope of the two regression lines for motion in the fixed and manipulated eyes was significantly larger in the high-versus low-awareness data, ANCOVA, coherence ¥ awareness interaction, F(1, 451) = 4.10, p < 0.05. Our findings thus indicate that awareness (or attention) can boost mean dominance durations and the effect of motion coherence on those dominance durations.

Covariation of changes in dominance and awareness

We also tested if dominance switches and changes in awareness had any temporal relationship to one another. In all subjects, there was indeed a correlation between the timing of the onsets and offsets of the awareness intervals and the dominance switches (BE tests, p < 0.01; Materials and methods). This is illustrated in the cross-correlograms of Figure 4A in which the density of awareness onsets (Figure 4A1) and offsets (Figure 4A2) is plotted as a function of time for one of the coherence conditions (90%). Note that there was a clear peak in the occurrence of awareness onsets immediately after the dominance switches (Figure 4A1, lag time about 150–400 ms) while the occurrence of awareness offsets clearly peaked just before these switches (Figure 4A2; lead time about 200–500 ms). Both effects were contrast dependent with the weakest and strongest coincidences occurring in the low- (light gray) and high- (black) contrast conditions, respectively. Similar results were obtained for the other coherence conditions (not shown). These findings suggest that dominance changes tend to trigger awareness while loss of awareness or attention, in turn, tends to trigger a dominance change. An alternative interpretation, however, is that these events are caused by a common mechanism. Adaptation reciprocal-inhibition models (Blake, 1989; Freeman, 2005; Lehky, 1988; Noest et al., 2007; Wilson, 2003) suggest, for example, that switches arise from adaptation of the currently dominant population and recovery of the suppressed population. It is conceivable, therefore, that awareness is more easily lost at the end of a dominance epoch due to progressive adaptation of the dominant population and that, at the moment of the switch, awareness is more easily (re)gained because the now dominant population has recovered from its previously adapted state. If so, one would expect that changes in awareness probability are phase locked to the dominance switches. We, therefore, analyzed the awareness probability as a function of normalized time in the two respective dominance epochs. In the resulting phase plots (Figure 4B), negative phase values correspond with dominance of the motion direction in the ipsilateral eye, and positive phase values correspond with dominance of the other eye’s motion direction. Note, there was a strong periodic modulation of the awareness probability, ANOVA, main effect of phase: F(71, 4211) = 1.73, p < 0.001. Typically there was an abrupt drop in awareness probability just before the occurrence of a dominance switch, which was then followed by a somewhat more gradual increase in awareness probability over the course of the subsequent dominance epoch. The magnitude of this modulation varied with stimulus contrast, ANOVA, main effect, F(2, 4211) = 3114.37, p < 0.001, and coherence, ANOVA, main effect, F(3, 4211) = 42.65, p < 0.001, but the shape of the normalized time courses was remarkably similar, ANOVA, phase ¥ contrast interaction, F(142, 4211) = 0.46, p > 0.99; phase ¥ coherence interaction, F(213, 4211) = 0.16, p > 0.99; and phase ¥ contrast ¥ coherence interaction, F(426, 4211) = 0.17, p > 0.99. In fact, it appeared that even in the high-contrast condition, subjects generally claimed being unaware of visual motion at the time of a dominance switch. One might worry that this striking result could be due to some movement coordination problem, forcing our subjects to transiently release the middle mouse button to indicate a dominance switch on the other two buttons, but this was not the case: Our subjects did not report such coordination problems on debriefing, and for the vast majority of switches, releases of the middle button and presses of that same button did not coincide within a 2-s time window around the switch (not shown).

Given that awareness onsets tend to be preceded by dominance switches, one might wonder how far into a
given awareness epoch switches occur. Figure 5 therefore examines how the distribution of dominance switches changed over the course of the two awareness states (i.e., aware vs. unaware) by plotting the average switch counts as a function of their normalized timing relative to the awareness onsets (at phase 0) and offsets (at phase −1 and +1). Although the switch densities (in counts per phase bin) were significantly modulated by the awareness phase, ANOVA, main effect, \( F(71, 4211) = 1.4, p < 0.02 \), stimulus contrast, ANOVA, main effect, \( F(2, 4211) = 8.7, p < 0.001 \), and motion coherence, ANOVA, main effect, \( F(3, 4211) = 7.01, p < 0.001 \), the overall picture is that switches occurred throughout the two awareness states. There seems to be some contrast-dependent phase locking, but this is at least partly explained by contrast-induced changes in awareness durations. For example, in the high-contrast conditions, awareness durations were comparatively long (not shown), making it likely that a switch occurs within that phase while it becomes unlikely that a switch occurs in an unaware epoch. This explains why the switch density is low during the unaware state and comparatively high for the aware state.

Discussion

In theory, it is possible that, due to the shorter lifetimes of the noise dots compared with the signal dots (Materials and methods), the decreases in coherence also reduced the effective contrast of the manipulated motion pattern. Note, however, that this possible side effect does not affect the interpretation of our results because it would merely contribute to the intended monocular decrease in “stimulus strength.” Our data suggest that this contribution is in fact negligible because the mean visual awareness levels were not significantly influenced by changes in motion coherence (Figure 1C).

One might suspect that subjects made more errors in correctly identifying the direction of motion in the currently dominant eye as reducing stimulus contrast decreased the motion awareness level. Note, however, that an increased tendency to perform at chance level should have influenced the dominance durations of both directions of motion. The same prediction holds for the influence that contrast might have had on the processing (Krekelberg, van Wezel, & Albright, 2006) and perception of stimulus speed (Thompson, Brooks, & Hammett, 2006). Instead, we found that the relationship between motion coherence in the manipulated eye and mean dominance duration of the motion direction presented in that same eye was remarkably invariant to the changes in contrast (Figure 2B, dashed lines), ANCOVA, coherence × contrast interaction, \( F(2, 794) = 1.41, p > 0.24 \). This supports the conclusion that the influence of contrast on the systematic changes in mean dominance duration of motion direction in the fixed eye (Figure 2B, solid lines), ANCOVA, \( t(2) = -11.86, p < 0.001 \), are not an artifact of changes in falsely identified motion directions or modifications in speed tuning but instead reflect true changes in the dynamics of eye dominance alternations.

Previous experiments in which binocular rivalry was studied with static orthogonal gratings have shown that binocular rivalry is replaced by superposition of the two images into a plaid percept if the contrast of the gratings is low (Liu, Tyler, & Schor, 1992). A major concern with interpreting our data as resulting from eye dominance alternations is therefore that the two dichoptic motion patterns might have fused. In this case, decreasing the motion coherence in one eye would attenuate the strength of this motion signal in the fused image, so one might expect a decrease in dominance of the corresponding motion direction—the pattern observed in Experiment 1. Our subjects were unable to discern whether fusion occurred. To rule out this possibility, we therefore tested if one of the two rivalrous motion patterns underwent suppression even if subjects had no visual motion awareness using a probe detection task.

Experiment 2: Probe detection

Paradigm

In the second experiment, we probed the strength of suppression of the nondominant motion pattern in four subjects who also participated in Experiment 1. Suppression strength of an image in one eye is usually determined by measuring the detection threshold for a brief probe stimulus presented to one eye while its image is suppressed and comparing that threshold to the threshold for detection of those probes in the same eye while its image is dominant (Fox & Check, 1968). In our study, the probe was a square patch of moving stimulus dots in the center of the right eye’s motion pattern (Figure 6A). The probe was presented either in the dominance or suppression phase for which no visual motion awareness was indicated.

The probe-detection task was adopted from Stuit et al. (2009) and modified for our purpose. Stimulus contrast was identical to the lowest contrast level of Experiment 1. Motion coherence was kept fixed at 100% in both eyes. Subjects were instructed to perform the same two tasks as in Experiment 1 (Figure 6A1) until a few switches in motion-direction dominance had occurred. Then, approximately 0.5–1.0 s after the onset of the next dominance epoch and in the absence of
visual motion awareness, a short beep was sounded. This beep was immediately followed by a $2^\circ \times 2^\circ$ square probe in center of the right eye’s image (Figure 6A2). The trial continued, and subjects then had to indicate whether they did or did not see a probe by pressing either the right or the left button, respectively (Figure 6A3). This button press terminated the trial.

The probe consisted of moving stimulus dots that underwent a transient luminance increase. No dots were added to the display. Only the luminance of stimulus dots moving within the probe area was first increased and then decreased to the baseline level along a Gaussian profile. This was done with the right eye’s motion pattern either in the dominant or suppressed state. The Gaussian envelope had a standard deviation of $57 \text{ms}$ and was truncated at $3.5 \text{SD}$ ($\text{SD}$ for $200 \text{ms}$). The amplitude of the Gaussian corresponded to the probe’s contrast and was varied across 40 trials using the adaptive Quest procedure (Watson & Pelli, 1983) implemented in the Quest toolbox (Department of Psychology, New York University) extension for Matlab.

**Data analysis**

The dependent variable was the probe contrast required to perform the probe detection task at 75% correct when motion direction in the right eye was either dominant or suppressed. These thresholds were determined using the adaptive Quest procedure (Watson & Pelli, 1983) and compared for the dominant and suppressed state using Student’s $t$ tests.

**Results**

Figure 6B plots the subjects’ (S1–S4) thresholds for the probe-detection task when motion direction in the probed eye was either in the suppressed (gray circles) or dominant (black circles) state. The results indicate that the contrast sensitivity for detection of the probe was significantly lower when the motion pattern in that eye was suppressed compared with when it was dominant, paired $t$ test, $t(3) = 3.97, p < 0.025$. In all our subjects, this loss of sensitivity in the eye with the suppressed motion pattern was on the order of 0.6–0.7 log units, which is quantitatively consistent with previous studies (Blake & Fox, 1974; Fox & Check, 1968, 1972; Nguyen et al., 2003) reporting a partial loss of contrast sensitivity of 0.3–0.7 log units for high-contrast stimuli. Our findings thus show that random dot motion stimuli still elicit eye dominance alternations even if their contrasts are too low to support visual awareness.

**Discussion**

Results from monocular probe-detection tasks are generally interpreted as the ability of the visual system to process a currently suppressed stimulus, reminiscent of the blindsight effect in neurological
patients (Weiskrantz, 1998). However, an alternative interpretation could be that presentation of the probe itself disrupts the image suppression and causes a reversal of rivalry dominance between the two eyes (Baker & Cass, 2013). Recently, Baker and Cass tested this notion by measuring both probe-detection accuracy and subjective confidence in those judgments (as a measure of awareness given by a binary response at the end of each trial). They found that subjects performed a probe-detection task with high accuracy but low confidence, indicating that the differences in sensitivity between the suppressed and dominant state proved a measure of the suppression depth.

In our Experiment 2, the probe was presented solely if subjects explicitly indicated that they had no motion awareness whatsoever. Moreover, a probe presentation closely followed the onset of a dominance epoch (see paradigm) when both the sensitivity to a probe (Alais, Cass, O'Shea, & Blake, 2010; Baker & Cass, 2013) and the awareness of a stimulus (Baker & Cass, 2013) were low in the suppressed eye. Our data, thus, corroborate the notion by Baker and Cass and provide novel evidence that interocular suppression does not require visual awareness of the image in the dominant eye.

General discussion

Binocular rivalry is generally considered a suitable tool for investigating the neural correlates of visual awareness because it involves changes in dominance and suppression of the retinal input without any change in those inputs (Leopold & Logothetis, 1996). Our current findings call for some caution. Our subjects reported that they were almost always unaware of any motion in the applied low-contrast stimuli, yet their motion-direction judgments alternated stochastically between the opponent motion patterns in the two eyes (Figure 1). We obtained crucial evidence that these alternations were at least partly induced by the same binocular rivalry mechanism that drives the alternations at higher contrasts. First, we found that the systematic changes in dominance alternations, which resulted from motion coherence manipulations in one eye, were qualitatively similar for the low-, medium-, and high-contrast conditions and fully consistent with L2 regardless of whether the subjects were aware of any motion in the stimulus patch or not (Figure 2). Second, we found that competing, low-contrast motion stimuli were able to induce a significant amount of interocular suppression even if the subjects were completely unaware of visual motion in those stimuli (Figure 6). We thus obtained the first empirical evidence that the dynamic process of dominance and suppression that underlies binocular rivalry also takes place in the absence of visual awareness.

Note, however, that these findings do not imply that visual awareness has no influence on the dominance alternations or that their time courses are independent. In the low-contrast condition, the changes in mean dominance durations of motion direction of the contralateral eye were steeper if the data were pooled across aware and unaware states (Figure 2B, light gray solid curve) compared with the data from the unaware states only (Figure 2D, solid curve). This suggests that the level of visual awareness does affect the rivalry dynamics. The results from the medium-contrast condition, for which we could split the dominance epochs into sizable groups with high- and low-awareness fractions, corroborate this notion (Figure 3); both the mean dominance durations as well as the effects of motion coherence on those dominance durations were boosted for the high-awareness epochs.

Although it has been shown that awareness and attention can be partially or fully dissociated either at the behavioral (Kentridge, Nijboer, & Heywood, 2008; Koch & Tsuha, 2007; van Boxtel, Tsuha, & Koch, 2010) or at the neural (Schurger, Cowey, Cohen, Treisman, & Tallon-Baudry, 2008; Wyart & Tallon-Baudry, 2008) level, it is widely believed that attention may be a prerequisite for perceptual awareness, meaning that in order to consciously experience a stimulus one must pay attention to it (Sergent, Baillet, & Dehaene, 2005; Sergent & Dehaene, 2004). On the other hand, several studies have shown that attention can indeed modulate binocular rivalry at least to some extent (Chong, Tadin, & Blake, 2005; Lack, 1973, 1978; Meng & Tong, 2004; Meredith & Meredith, 1962; Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999; van Ee, van Boxtel, Parker, & Alais, 2009; van Ee, van Dam, & Brouwer, 2005). Moreover, despite the fact that both behavioral (Pastukhov & Braun, 2007) and neural (Roebor, Vser, Shgroer, & O'Shea, 2011) evidence were presented that attention is not able to fully explain perceptual switches in binocular rivalry, recent findings suggest that binocular rivalry is abolished if attention is withdrawn from rivalrous stimuli (Brascamp & Blake, 2012; Zhang, Jamison, Engel, He, & He, 2011).

Note, however, that attention alone cannot account for the observed compliance with L2 (Figure 2) or the interocular suppression (Figure 3). These features are a hallmark of binocular rivalry (Blake, 2001, 2005) and are thought to result from cross-inhibition between rivalrous stimuli combined with neural adaptation and noise (Brascamp et al., 2006; Lankheet, 2006). Thus, although our findings can be interpreted as supporting the modulatory role of attention in binocular rivalry, they also suggest that cross-inhibition mechanisms play...
a crucial role in the neural competition process underlying multistable perception. This mechanistic interpretation of our results is supported by the strong suppression of awareness that we observed at the time of a switch (Figure 4). This is the kind of suppression one would expect if dominance switches were produced by a competition-adaptation mechanism, such as proposed by classic adaptation mutual-inhibition models (Blake, 1989; Freeman, 2005; Lehky, 1988; Noest et al., 2007; Wilson, 2003). Due to the adaptation of the currently dominant population over the course of the dominance interval, the activity levels of that population will gradually decline, making the end of that dominance epoch the most likely point in time for the activity levels to drop below the awareness level. Immediately after the dominance switch, however, the now dominant population has recovered most from its previous adaptation and is therefore most active, rendering the beginning of a dominance epoch the most likely point in time to (re)gain awareness of the stimulus. This interpretation is in line with recent findings that the sensitivity for probe detection over the course of a dominance interval decreases in the dominant eye as a result of adaptation and increases in the suppressed eye as a result of recovery from adaptation (Alais et al., 2010).

The ability of the brain to process visual information in the absence of visual awareness is reminiscent of other experimental and clinical studies in which an uncoupling between visual awareness and visually guided behavior is observed. Clinical studies indicate, for example, that patients with lesions restricted to the primary visual cortex (V1) are still able to perform visually guided tasks correctly even though they are entirely unaware of the stimuli to which they are responding, a phenomenon known as blindsight (Weiskrantz, 1998). Similar results were obtained from neurologically normal human subjects with V1 deactivates by the transcranial magnetic stimulation (Boyer, Harrison, & Ro, 2005) and animals with surgically removed V1 (e.g., Cowey & Stoerig, 1995; Feinberg, Pasik, & Pasik, 1978; Isa & Yoshida, 2009; Moore, Rodman, Repp, & Gross, 1995). Visual task performance and visual awareness can also be dissociated in normal observers using visual masking (e.g., Kolb & Braun, 1995; Meeres & Graves, 1990). Pattern masks that follow the onset of a test face-stimulus interrupt firing of face-selective neurons in the inferior temporal cortex of macaques (Rolls & Tovee, 1994; Rolls, Tovee, & Panzeri, 1999). Under the same conditions, human observers did not have full conscious perception of the faces and felt, as in blindsight, that they were guessing even though their performance was well above chance (Rolls, Tovee, Purcell, Stewart, & Azzopardi, 1994). It was therefore suggested that a rather strong signal is required to overcome a threshold for access to the conscious processing system (Rolls & Deco, 2002). This notion is further supported by fMRI data indicating that dichoptic masking correlates with visual awareness only in ventral stream areas beyond area V2 (Tse, Martinez-Conde, Schlegel, & Macknik, 2005). In terms of binocular rivalry, this would mean that the activation needed for alternating dominant states to guide behavior might be lower than the level necessary for visual awareness. It is also possible that the integration time constants for visually guided decision making (Ditterich, 2006) are longer than the ones that determine the momentary content of visual awareness.

In summary, by introducing monocular motion coherence manipulations into the binocular rivalry paradigm and by probing the strength of the interocular suppression induced by competing, low-contrast motion stimuli, we have shown, for the first time, that ocular dominance rivalry does not require visual awareness. We also found that fluctuations in awareness that did occur were temporally linked to the dominance switches in a manner that is consistent with adaptation reciprocal-inhibition models of binocular rivalry. These discoveries might be interpreted as evidence that binocular rivalry is resolved at low levels of visual processing (Blake, 1989; Lehky, 1988; Tong, 2001). Note, however, that areas in the ventral pathway are believed to mediate visual perception (Blake & Logothetis, 2002; Logothetis, 1998; Wilke, Logothetis, & Leopold, 2006) and represent a stage beyond the resolution of ambiguities during binocular rivalry (Sheinberg & Logothetis, 1997). Areas in the dorsal pathway, on the other hand, are thought to control visually guided actions, processing information of which we are unaware (Fang & He, 2005; Milner & Goodale, 1995). Our findings thus add to the literature proposing that binocular rivalry and multistable perception, in general, might instead find its origin in frontoparietal decision-making processes that guide behavior (Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Leopold & Logothetis, 1999; Lumer, Friston, & Rees, 1998; Rees, 2001; Ricci & Blundo, 1990; Sterzer, Russ, Preibisch, & Kleinschmidt, 2002).

Keywords: binocular rivalry, bistable perception, dominance alternations, visual awareness

Acknowledgments

This work is supported by NWO Grant 864.06.005 (ALW VIDI) and the Radboud University Nijmegen Medical Centre.

Commercial relationships: none.
Corresponding author: Jeroen Goossens.
References


