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Contradictory influence of context on predominance during binocular rivalry

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Background: Binocular rivalry is a complex process characterised by alternations in perceptual suppression and dominance that result when two different images are presented simultaneously to the left and right eyes. It has been reported recently that the addition of contextual cues will promote the predominance of the context consistent rivalry target. In contrast to Levelt's second proposition (1965), this effect has been found to result exclusively from an increase in the dominance phase duration, while the suppression phase duration remains unaffected.
Methods: Human subjects were simultaneously presented with a small (2°) disc consisting of gratings (four cycles per degree) of different orientations to the two eyes. Four experiments were conducted to ascertain the effects of background gratings and contextual colour information on target predominance and phase duration. For each of the four experimental conditions, the orientation and colour of the target gratings and surrounding contextual background were systematically manipulated.
Results: In this study, we report an effect opposite to that of Levelt. Contradictory contextual information increases target predominance and phase duration during binocular rivalry. Our results demonstrate that it is possible to promote the dominance of the context contradictory percept with co-linearity, co-chromaticity and orientation cues. In line with previous studies involving context, we find that this effect on predominance is due to an increase in the duration of the dominance rather than the suppression phase.
Discussion: We discuss our findings in respect to those from previous studies and consider high- and low-level processes that may be responsible for these apparently 'contradictory' roles of context on binocular rivalry. In addition, we discuss how the apparent 'anti-Levelt' effect of context can be reinterpreted in a manner that brings it back in line with Levelt's second proposition and raises the question of whether 'suppressability' plays a disproportionately large role in determining the duration of perceptual phases in binocular rivalry.

Key words: binocular rivalry, context, dominance, suppression

The human brain faces an epic task in visual perception; it must construct the image that we perceive from an object's often ambiguous retinal projection. In nearly all situations, this construction is performed seamlessly but in certain circumstances, it is possible to force the brain into revealing details about this process. The alternations in perception during binocular and perceptual rivalry reveal an inability of the brain to construct a single, coherent image from its sensory input. Instead it oscillates between the two equally parsimonious percepts that may be constructed from the raw afferent input.[1,2]

Although the neural underpinnings of binocular rivalry are still the subject of much debate,[3-6] it is now clear that in many circumstances image coherence is favoured over eye-of-origin cues.[3,7-9] What is not so clear is whether there is the same preference for coherence between a given rivalry target and the background within which it is set.

Central to the construction of any percept is figure-ground segregation; the segregation of objects from their background. The importance of visual-feature binding in this process has been appreciated since the time of the early Gestalt psychologists[10] and numerous cues, which might underlie such binding, have been proposed, such as surface luminance, and the geometry of surfaces such as their collinearality, motion contrast and orientation contrast (see review[11]). In a series of experiments, Alais and Blake[12] revealed that Gestalt binding affects rivalry by driving the construction of alternative, refined percepts, which then undergo binocular rivalry. Two gratings with orthogonal, parallel (without continuity) or collinear lines were presented to the subject's left eye and were paired with two random dot patterns presented to the complementary regions of the right eye. As expected, the binding cues significantly increased the joint predominance of the collinear gratings. It has also been shown that a target will dominate if it is consistent with external contextual cues, such as global motion[12,13] and depth from shading cues.[13] On the basis of such findings, it has been implied recently in the literature that the exclusive effect of context is to enhance predominance of the consistent rivalry target.[13,14] The purpose of this study was to ascertain whether context could similarly be shown to enhance predominance of the 'context-contradictory' target.

One important feature of binocular rivalry is that by manipulating the stimulus properties it is possible to cause predictable changes to the duration of perceptual dominance or suppression phases.[15] For a number of years it has been known that manipulating the 'strength' of one of the rivalling figures through increases in motion,[16] contrast[17] and spatial frequency[18] will affect the overall predominance. However, it was Levelt[15] who showed that such stimulus manipulations always lead to a reduction in the duration of suppression, rather than an increase in the dominance intervals of that stimulus. This effect, often referred to as Levelt's second proposition of binocular rivalry, until recently was considered a fundamental characteristic of binocular rivalry. Therefore, it was of particular interest when it was revealed that the addition of contextual information has the opposite effect, acting to increase the length of the perceptual dominance phase. To date, this anti-Levelt effect of context has been reported to increase the dominance of the 'context-consistent' stimuli.[12,13,19]

In this study, we show that context can influence binocular rivalry in a number of seemingly contradictory ways. The first effect involves the background on which the rivalrous components of the stimulus are placed. Here we present results that indicate that during binocular rivalry, contextual cues such as collinearity, cochromaticity and orientation can act to promote increased dominance of the 'context contradictory' percept. These findings are in contrast to those reported in the current literature but are in line with work done more than a decade ago.[20-22] The second effect of context that we report refers to the grouping/binding of an object on the basis of contextual information within the stimulus. In our study, we found that compatibility cues did influence the binding/grouping of discrete rivalrous targets of a stimulus, leading to an increase in the proportion of synchronised dominance and suppression of the compatible regions. However, again the degree of predominance was found to be consistently biased toward the synchronised dominance of the context-contradictory targets. We discuss these findings in respect to psychophysical and neurophysiological studies that suggest how differences in the proximity of contextual information could be responsible for the discrepancy between our results and those reported previously.

EXPERIMENT 1. CONTEXT PROMOTES THE DOMINANCE OF ORTHOGONAL STIMULUS

In the process of an ongoing study being conducted in the laboratory, we undertook experiments using binocular rivalry stimuli loosely based on the one described by Blake and Logothetis.[14] Contrary to our expectation of an increase in the predominance of the 'context-compatible' target, we found subjects reported an increase in the 'context-contradictory' target. The current study was designed to investigate these reports more formally.

Methods

OBSERVERS

Two of the authors (OC and TC) and four naive individuals volunteered as participants in this study. The naive subjects for this and the three subsequent experiments were either students or employees of The University of Queensland, with normal or corrected to normal vision (6/9 or better) in each eye. This study was approved by The University of Queensland Behavioural and Social Sciences Ethical Review Committee.

APPARATUS AND STIMULI

For the control condition one eye was presented with a grating consisting of equal width green and black square wave gratings, oriented with a rightward slant of 45°. The other eye was presented with a similar grating but with a leftward (-45°) slant. The gratings were presented as a disc that subtended 2° of visual angle and had a spatial frequency of four cycles per degree. Using a VisionWorks package the stimuli were displayed on an ultra-short persistence monochrome computer monitor (green, P46 phosphor persistence = 65 nsec) and viewed from a distance of 60 centimetres. The leftward and rightward oblique gratings were presented alternately, in rapid succession, at a rate of 120 Hz. Subjects viewed the display through liquid crystal shutters that alternately blocked presentation to the left and the right eye in synchrony with the stimuli. Using this method it was possible to

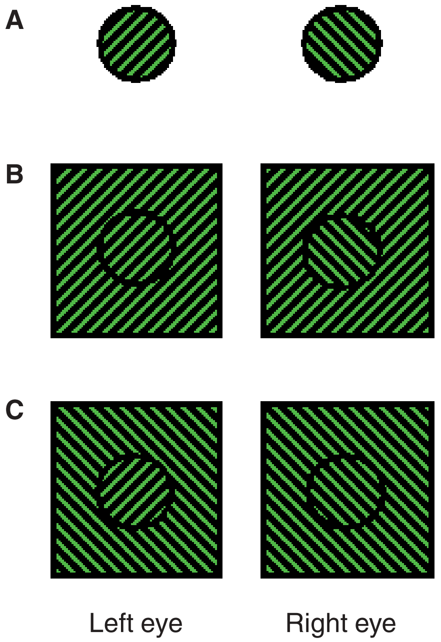

Figure 1. Stimuli used in Experiment 1. (A) In the control condition subjects were simultaneously presented with a disc of rightward (45°) tilting gratings to one eye and leftward (-45°) tilting gratings to the other eye. The same circular patches were presented on (B) a background of rightward tilting gratings for the first experimental condition and (C) a background of leftward tilting gratings for the second experimental condition.

present the conflicting stimuli to the corresponding retinal location of each eye, without perceptual flicker or cross-talk.

For the first experimental 'context' condition, we used a display that was exactly the same as that used in the control condition, except that each circular grating was presented on a background (6° x 6° of visual angle) consisting of a slanted grating of exactly the same colour, orientation and spatial frequency as the rightward slanted grating. In the second experimental condition, the contextual background was consistent with the leftward slanting gratings. In both cases, the circular patches were bordered by a black ring (0.1° of visual angle) so that they were clearly dissociable from the background (Figure 1).

Data for each control and experimental condition were collected using commercial software (Bireme.com.au) over a 10-minute period consisting of four 100-second trials, with subjects receiving a 30-second break between each trial. Responses were recorded on a modified computer keyboard. Two raised buttons, one with a ridge angled at 45° and the other angled at -45°, were placed on top of the B and V key respectively. All tests were carried out in a dimly lit, quiet room and the eye and order of presentation for each of the tests were counterbalanced.

PROCEDURE

Under all conditions, subjects were instructed to focus only on the orientation of the gratings within the circular patch. Subjects were asked to report the predominance of the rightward gratings by pushing the button with the corresponding 45° angled ridge and the predominance of the leftward gratings by pushing the button with the corresponding -45° angled ridge. If the subject experienced a combination of the two orientations, as either a grid or a patchwork, they were instructed to press the space bar. Periods during which the spacebar was pressed were removed before analysis

STATISTICAL ANALYSIS

The dependent variable in this experiment was predominance of the rightward slanting gratings. This was calculated by dividing the total time during which a subject reported seeing the 45° target by the total time they reported seeing either the -45° or the 45° target. The calculated value was then transformed into a percentage. Mean phase duration was the average duration of time (seconds) that the subject reported uninterrupted dominance of the respective target. Significance was subsequently measured using a repeated measure analysis of variance (ANOVA), with a planned comparison between predominance of the 45° target under control and the respective experimental conditions.

Results and discussion

Under both experimental conditions, the addition of contextual information was found to increase significantly the predominance of the orthogonal grating. Under the control (no context) condition there was no overall bias in the predominance of 45° (μ = 51.75%, σ = 5.50%) and -45° (μ = 48.25%, σ = 5.50%) gratings. When the same stimulus was presented within a context of either leftward or rightward slanting gratings, there was a significant increase in predominance of the rivalry target oriented orthogonally to the background. Within a context of 45° gratings, the 45° target predominated (μ = 60.78%, σ = 7.89%; $F_{(1,5)}$ = 125.42, $p < 0.01$), while a context of 45° promoted the predominance of the orthogonally aligned 45° target (μ = 65.23%, σ = 5.81%; $F_{(1,5)}$ = 22.01, $p < 0.01$) (Figure 2a).

In both conditions, this increase in predominance of the orthogonal target was due to a direct increase in the dominance duration of that target. The mean dominance duration of the 45° target (control: μ = 1.90 sec, σ = 0.35 sec) was unaffected by the addition of the relatively collinear 45° context (μ = 1.83 sec, σ = 0.29 sec; $F_{(1,5)}$ = 1.38, NS) but significantly increased within a context of -45° gratings (μ = 3.01 sec, σ = 0.47 sec; $F_{(1,5)}$ = 28.19, $p < 0.01$). Likewise the mean dominance duration of the -45° (control: μ = 1.80 sec, σ = 0.37 sec) was significantly greater with the 45° context (μ = 2.90 sec, σ = 0.87 sec; $F_{(1,5)}$ = 21.13, $p < 0.01$), but was unaffected by the addition of -45° gratings (μ = 1.66 sec, σ = 0.32 sec; $F_{(1,5)}$ = 0.49, NS) (Figure 2b). This result is contrary to the observations made by Levelt[15] but in line with previously reported effects of context.[12,13]

EXPERIMENT 2: THE EFFECT OF COLOUR

The results from Experiment 1 show a clear effect of context that is opposite to that which is being reported in the current literature. However, as the experiment used a novel stimulus, it was not possible to determine whether the effect observed was unique to the stimulus or representative of the general nature of contextual interactions. As colour has been shown to influence binding and grouping within an object[23] and to affect

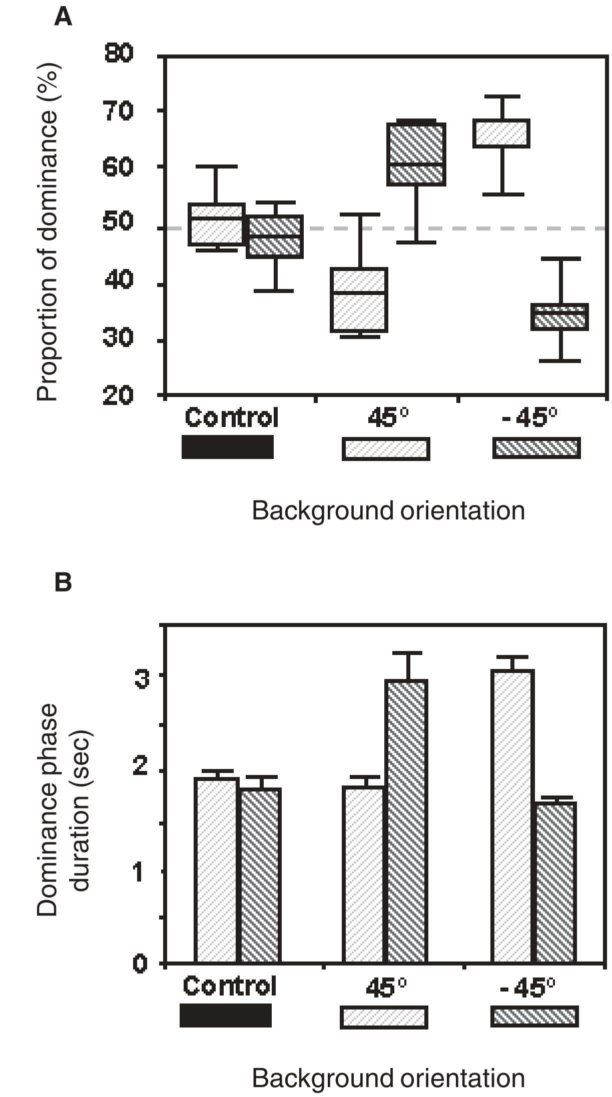

Figure 2. The effect of contextual orientation cues on the predominance of rivalry targets. (A) The predominance (%) of the 45° rightward (light grey) and -45° leftward (dark grey) tilting gratings under control and contextual conditions. In each boxplot, the inner line and the upper and lower sides of the box represent the median and the first and third quartile values, respectively, while the whiskers extend out to the minimum and maximum data values. Compared to the control (no context) condition, presentation of the rivalry targets within a context of 45° gratings was found to increase significantly the predominance of the orthogonal -45° target. Similarly, the -45° context promoted the predominance of the orthogonal 45° target. (B) The mean dominance phase duration for the 45° and -45° targets under the control and context conditions (standard error is depicted by the vertical bars). Only the dominance duration of the orthogonal target was found to be effected.

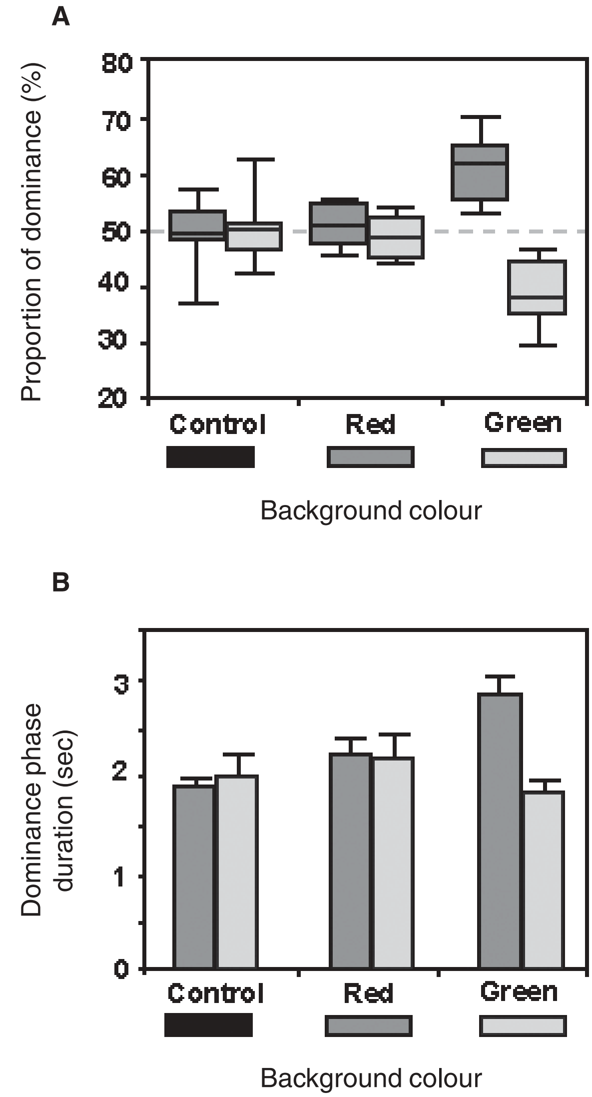

Figure 3. The effect of contextual colour cues on the predominance of rivalry targets. (A) The predominance (%) of the red and green oblique gratings under control and context conditions. Compared to the control (no context) condition, presentation of the rivalry targets within a solid green background was found to increase significantly the predominance of the contrasting red target. However, the addition of a solid red background had no effect on target predominance. (B) The mean dominance phase duration for the red and green targets under the control and context conditions (standard error is depicted by the vertical bars). The addition of the green context increased the dominance duration of the red target, while addition of the red context had no effect.

dominance and suppression phases during binocular rivalry,[24] we were interested to see if the effect observed in Experiment 1 would be diminished or enhanced with the addition of colour. The following experiment was designed to investigate the influence of contextual colour information on the suppression and dominance phases of binocular rivalry.

Methods

Two of the authors (OC and TC) and four new naive individuals volunteered for this study. All subjects had normal or corrected to normal vision (6/9 or better) in each eye and while colour vision was not tested explicitly, all subjects reported the red and green target colours to be clearly distinguishable.

The control for this stimulus was the same as that described in Experiment 1, except that the oblique gratings were coloured red and green, respectively. The stimuli were presented on a BARCO 808s stereo capable analogue projector with fast red and green phosphotubes (red persistence 2 ms, green 1.65 ms) and subjects viewed the display through liquid crystal shutters.

The 'colour context' stimuli were the same as those used in the control condition, except that the rivalry targets were presented on a background of solid red (subtending 6° x 6° of visual angle) in the first experimental condition and on a background of solid green in the second condition. To control for any confounding influence of orientation, the red and green target gratings were oriented at 45° and -45° respectively for half of the subjects; for the other three subjects this orientation was reversed. For all subjects, the eye of presentation was reversed after two of the four trials and the order of stimulus presentation was counterbalanced.

Under all conditions, subjects were instructed to focus on the orientation, rather than colour, of the gratings within the circular patch. Subjects were asked to report the predominance of the rightward gratings by pushing the button with the corresponding 45° angled ridge and the predominance of the leftward gratings by pushing the button with corresponding -45° angled ridge. For statistical analysis, the dependent variable in this experiment was predominance of the red slanting gratings. All other aspects of the procedure and statistical analysis were the same as described in Experiment 1.

Results and discussion

The predominance of the coloured target gratings was affected by the addition of the green but not the red contextual background. Under the control (no context) condition there was no overall bias in the predominance of the red (μ = 49.38%, σ = 6.97%) and green (μ = 50.62%, σ = 6.97%) gratings. When the same stimulus was presented within a context of solid green colour, the red gratings predominated (μ = 61.23%, σ = 6.16%; $F_{(1,5)}$ = 26.58, $p < 0.01$). The addition of a red context was found to have no effect, however, with the green gratings showing no predominance (μ = 49.05%, σ = 3.91%; $F_{(1,5)}$ = 0.592, NS) (Figure 3a).

Consistent with the results of Experiment 1, the increase in predominance of the red target by the addition of green contextual cues was due to a direct increase in the mean dominance duration of the red target. Compared to the control condition, the addition of a green background had no effect on the mean dominance duration of the green target (control: μ = 1.97 sec, σ = 0.99 sec; green context: μ = 1.81 sec, σ = 0.50 sec; $F_{(1,5)}$ = 0.62, NS) but significantly increased the mean dominance duration of the red target (control: μ = 1.87 sec, σ = 0.51 sec; green context: μ = 2.82 sec, σ = 0.78 sec; $F_{(1,5)}$ = 26.58, $p < 0.01$) (Figure 3b).

The asymmetric effect of contextual colour was unexpected but interesting and warrants further investigation. Unfortunately, we did not test the observer's subjective levels of iso-luminance before participation in the experiment. However, given that the red and green targets showed equal predominance under the control (no context) experiment, we believe that our results do not reflect an inherent difference in the properties of the red and green colour used or in individual differences in red/green colour vision. Albeit entirely speculative, one possible explanation for our results may be an asymmetric salience of the red and the green backgrounds. In an evolutionary sense, one can imagine that the discrimination of red objects from a green (foliage) background would have been of greater significance than the discrimination of green objects from a red background. Irrespective of the validity of this speculative explanation, our results do highlight the need for a more thorough understanding of the role of colour in binocular rivalry and for future experiments conducted under controlled iso-luminant conditions.

EXPERIMENT 3: INTEGRATING PREVIOUSLY REPORTED FINDINGS

As the initial experiments were motivated by a discrepancy between our own observed effect of context and that described by Blake and Logothetis,[14] we felt that reconsideration of previously reported effects of context may help to clarify the issue. To this end we conducted a further two experiments. The first involved one of the stimuli described in the afore mentioned paper, while the second experiment was based on one of the experiments reported by Alais and Blake.[19]

Experiment 3a

Experiments 1 and 2 of the current study show that the dominance of a monochrome rivalry target can be promoted by a context of orthogonally oriented gratings, while a red target can be promoted by a green context. Given that the stimulus described in the review by Blake and Logothetis[14] consisted of a rivalrous patch of red vertical and green horizontal gratings on a contextual background of red vertical gratings, we considered that the difference in reported effects of context could reflect differences between the stimuli. The authors of the current study are aware that the stimulus described by Blake and Logothetis[14] was designed as a simplistic rather than a literal representation of a specific experimental stimulus, nevertheless, we were interested to determine the effect of the contextual condition that was described.

Methods

Two of the four authors (OC and TC) and six naive individuals volunteered as observers for this experiment. All subjects had normal or corrected to normal vision (6/9 or better) in each eye and reported clearly distinguishing the red and green target colours.

For the control condition, one eye was presented with red and black vertical gratings, while the other eye was presented with green and black horizontal gratings. For the 'context' condition, the control stimulus was viewed against a background of red and black striped vertical gratings, as described in Figure 2a of Blake and Logothestis,[14] otherwise the set-up was identical to that described in Experiment 2.

Responses were recorded on a modified computer keyboard. Two raised buttons, one with a ridge aligned vertically/perpendicular (0°) to the observer and the other running left to right (90°), were placed on top of the B and V keys, respectively.

Under both conditions, subjects were instructed to focus only on the orientation of the gratings within the circular patch. Subjects were asked to report the predominance of the vertical gratings by pushing the button with the vertical ridge and horizontal gratings by pushing the button with a ridge running from left to right. All other aspects of the procedure and statistical analysis were the same as described in Experiment 2.

Results and discussion

Consistent with Experiments 1 and 2, the addition of the contextual information was found to increase significantly the predominance of the contradictory target. Under the control (no context) condition, there was no overall bias in the predominance of red vertical (μ = 47.81%, σ = 12.82%) and green horizontal (μ = 52.19%, σ = 12.82%) gratings. However, when the same stimulus was presented within a context of red vertical gratings, there was a significant increase in the predominance of the green horizontal gratings (oriented orthogonally to the background) (μ = 66.78%, σ = 14.31%; $F_{(1,7)} = 21.77$, $p < 0.01$) (Figure 4). This result is the opposite of that reported in the review by Blake and Logothetis[14] but as the stimulus described in the review was never experimentally tested, we see no reason to question the validity of our own results.

As an aside, we considered that our findings reflected an effect of stimulus presentation rather than contextual cues. To rule this out we tested five subjects on the same stimulus described in Experiment 3 but under conditions of free fusion (data not shown). The effect was found to be attenuated but in the same direction as that described in the current study.

Experiment 3b

The results of Experiments 1, 2 and 3a show that when binocular rivalry occurs between targets located in a contextual setting, the context-contradictory target will dominate. As has been discussed, this finding stands in contradiction to a number of recent studies. However, all of the previous experimental studies that have shown that context increases the predominance of the consistent target, and involved either multiple rivalry regions or multiple, spatially separated contextual cues. Thus we were interested to investigate what would happen if multiple rivalry regions were presented within a contextual background that was coherent with one of the rivalling alternatives. This would provide both between target contextual information like that described by Alais and Blake[19] and external contextual cues, like the ones used in the previous three experiments. To test this we designed a stimulus with two separate but identical rivalrous regions set within a contextual background consistent with one of the rivalrous targets. We predicted that the contextual setting would promote the dominance of the context incongruent targets, while simultaneously the contextual grouping/binding cues would promote the synchronised dominance and suppression phases of the two regions. Consequently, it was expected that the most reported percept would be the synchronised dominance of the context contradictory targets, followed successively by the synchronised dominance of the context consistent targets and asynchronous dominance resulting in a mixed percept.

Methods

Two of the authors (OC and TC) and six naive individuals volunteered as observers in this experiment. The stimulus for the first experimental condition consisted of two rivalrous disks containing either vertical or horizontal green and black striped gratings (each subtending 0.5° of visual angle) and a fixation cross, overlaid on a background of vertical gratings. The disks were situated 0.75° (measured as vertical distance from the centre of the respective targets) below the fixation cross and separated by a centre-to-centre distance of 1° of visual angle. To ensure that synchronised dominance reflected grouping based on contextual cues rather than grouping due to a common eye of presentation, each eye was presented with one vertical and one horizontal grating target (Figure 5). The grating pattern of the disks had a spatial frequency of eight cycles per degree. All other stimulus parameters and the method of dichoptic presentation were the same as described in Experiment 1. The stimulus for the second experimental condition was identical, except that the circular patches were presented on a background of horizontal gratings.

Under both conditions, subjects were instructed to focus only on the orientation of the gratings within the two circular patches. Subjects were asked to report the joint predominance of the vertical by pushing a button with a ridge aligned perpendicular to the observer (0°), the joint predominance of horizontal gratings by pushing a button with a ridge running from left to right (90°) and any combination of vertical and horizontal by pushing an adjacent button that had no ridge. All other aspects of the procedure were the same as described in Experiment 1.

Results and discussion

Using two tailed t-tests for dependent samples, the effect of the contextual background on the proportion of synchronised predominance of vertical and horizontal gratings and the mixed predominance of targets was calculated. Embedded within a context of vertical gratings, synchronised predominance of the vertical targets was reported 6.97% (σ = 6.61%) compared to

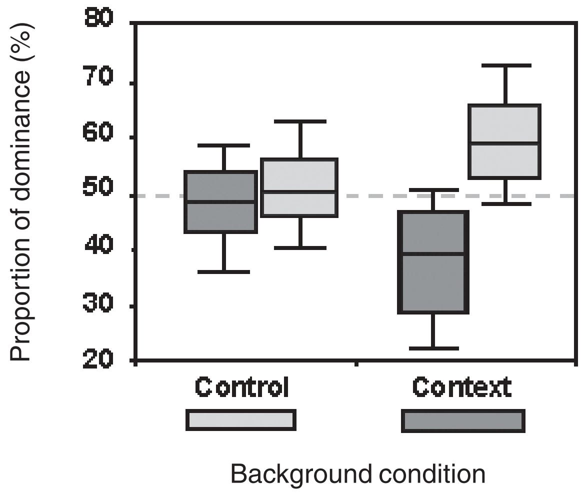

Figure 4. The effect of colour and orientation contextual cues on the predominance of rivalry targets using a stimulus like that described by Blake and Logothetis.[14] The box plots show the percentage of reported predominance of the red vertical gratings and green horizontal gratings under context and control conditions. In line with Experiments 1 and 2, the addition of the red vertical background gratings led to an increase in the predominance of the context 'contradictory' green horizontal target.

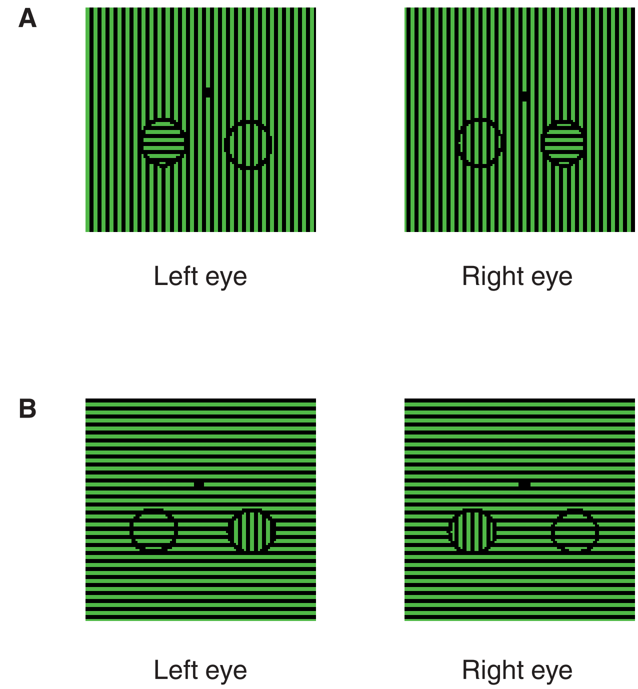

Figure 5. The stimuli used in Experiment 3b. (A) In the first condition, the rivalry targets, consisting of either horizontal or vertical gratings, were presented to the left and the right of a fixation cross on a background of vertical gratings. (B) In the second condition, the same rivalry targets were presented on a background of horizontal gratings.

64.13% (σ = 14.89%) of the test period, when the same targets were embedded within the 'orthogonal' context of horizontal gratings ($t_{(7)}$ = 8.55, $p < 0.01$). The complementary effect was observed with the synchronised predominance of horizontal targets. Within a context of 'orthogonal' vertical gratings, the joint predominance of horizontal targets was reported 69.75% (σ = 11.51%) compared to only 10.42% (σ = 11.76%) of the testing period, when the same targets were embedded within a 'consistent' context of horizontal gratings ($t_{(7)}$ = 9.15, $p < 0.01$). There was no effect of background orientation on the proportion of mixed predominance reported (vertical background: μ = 23.28%, σ = 8.76%; horizontal background: μ = 25.44%, σ = 14.44%; $t_{(7)}$ = 0.47 p = NS) (Figure 6).

In line with our predictions, the most reported percept was the synchronised dominance of the context contradictory targets. Against prediction, the mixed percept was experienced for a greater proportion of time than the joint predominance of the context consistent orientation. This result suggests that the cues driving binding of spatially separate rivalrous regions are largely overridden by the combined influence of 'environmental' context and eye of presentation cues.

GENERAL DISCUSSION

Summary and discussion of results

This study aimed to investigate the effects of context on binocular rivalry. Our results show that contextual information can serve to promote the predominance of the context contradictory target. While this is opposite to the effect of context currently being reported in the literature,[13,14] we do not feel that our results question the validity of previous studies but rather suggest that contextual cues can have two seemingly contradictory effects on rivalry predominance. Second, we found that this effect of context is mediated through an increase in the dominance phase of the predominant target. This finding is in line with previously reported contextual effects but appears to be in stark contrast to Levelt's second proposition,[15] which states that changes in the stimulus strength of one percept affects its periods of dominance, solely through reducing the dominance of the other percept.

Specifically, we considered the influence of collinear and co-chromatic background contextual cues. In Experiment 1, a rivalrous region consisting of leftward and rightward oblique gratings was presented within a contextual background of gratings contiguous with one of the rivalry targets. Under these conditions, the context-contradictory percept was always found to predominate. In contrast to the collinearity contextual cues in Experiment 2,

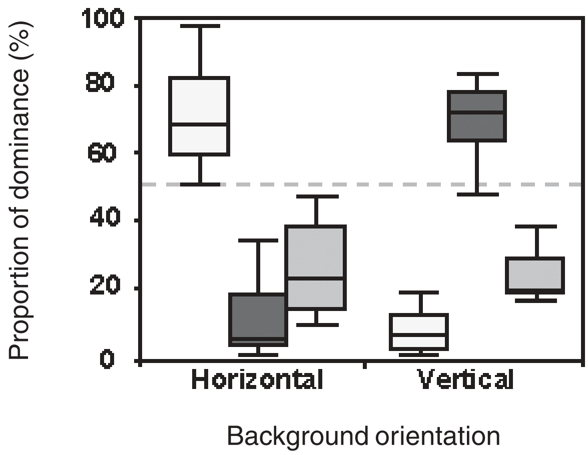

Figure 6. The effect of contextual background on the synchronised predominance of spatially separate rivalry targets. The percentage of mixed predominance (light grey), the synchronised predominance of the vertical targets (white) and the horizontal targets (dark grey). Irrespective of the orientation of the contextual background, the most reported percept was the joint predominance of the context 'contradictory' targets, followed by mixed target predominance. While the least experienced percept was the synchronised predominance of context consistent targets.

co-chromaticity cues were shown to have an asymmetric effect. When the contextual cues consisted of a green background, the red grating target predominated over the rivalrous green grating target, in accordance with our earlier findings. Interestingly, when the same rivalry targets were presented within a solid red background, no significant changes in the predominance were seen. One speculative evolutionary explanation for our results was that the red and green backgrounds were asymmetric salient context cues, given the evolutionary significance of tasks that involve the discrimination of red objects from a green (foliage) background, as opposed to the discrimination of green objects from a red background. While this result clearly requires further investigation under controlled iso-luminant conditions, such red-green asymmetries have been observed previously in binocular rivalry[25] and may provide fruitful avenues for future research.

We also show that when the stimulus consists of multiple spatially separated rivalrous regions, contextual cues promote the synchronised co-dominance of the context-contradictory targets. In addition, it was shown that the contextual cues promoting the predominance of the context contradictory target are stronger than those promoting the binding and co-dominance of the spatially separated regions.

Relating our results to previous findings

When our results are considered with respect to a number of recently published findings, it is clear that context can influence perceptual dominance at a number of levels and sometimes in seemingly contradictory ways. Experiments performed by Alais and Blake[19] and Sobel and Blake[13] demonstrate that compatible contextual information will drive entrained alternations between discrete rivalry targets in a manner similar to that which has been reported within regions of a single rivalry stimulus.[9,26] Where things become less clear is in identifying the role that context, external to the rivalry targets, plays on target predominance. In this respect, Sobel and Blake[13] showed that contextual information, spatially separated from the rivalry targets, can act to promote the dominance of the context consistent target. Here, we have shown that contextual information can also act to promote the dominance of the context-contradictory percept. We would like to point out that while our results are in the opposite direction to the main effect of context currently being reported, similar results have been shown in earlier experiments in which rivalrous targets were bordered by a textured annulus.[20-22] Therefore, the interesting question is: why do different types of contextual information have such seemingly contradictory effects on target predominance?

High level explanation: Monocular zones and object integration versus segregation

One possible, high-level explanation for our results would involve mechanisms that have evolved to cope with monocular zones in binocular vision.[27-29] Monocular zones are regions within the area of binocular overlap for which the two eyes receive different input due to the occlusion of one eye's view. As the eyes are separated, an object located in depth will occlude different portions of a scene in each eye. This phenomenon can be easily experienced by placing an object (for example your finger) a few centimetres in front of your face and fixating on a point in the distance, you will notice that you will see the object (your finger) in double. It is these regions that are considered monocular zones, because within these regions the view of the world is limited to the monocular input, that is, where one eye sees a finger, the other eye observes a view of the distant scene. In the contextual settings of our experiments, the 'context-contradictory' target may be construed as being a monocular zone occluded in the other eye.[30] The large patterned background may be seen as an occluding body and the circle surrounding the rivalrous region may be seen as either a hole through which one of the eyes can see or a small patterned disc situated close to one of the eyes. As monocular zones are important sources of visual information,[27,28,31] they may be preferentially viewed during binocular rivalry. This preference for perceiving the monocular zones depends on an interpretation of the ecological significance of the rivalrous percepts.[32] This interpretation is consistent with our own finding that a green but not red background promoted the predominance of the incongruent rivalry target. Given the ecological salience of a green background for our forest-dwelling ancestors compared with the low likelihood of an ecologically valid red background, it is conceivable that through the course of evolution these two colours have attained asymmetric significance or influence on the competing dominance of monocular zones.

In contrast, there are no conditions of occlusion that could generate retinal input like the one presented by Sobel and Blake.[13] In fact in their experiment, the grey background provides an illusion of occlusion necessary to generate the appearance of coherent motion between spatially separated regions. In this case, the monocular zone itself cannot correspond to an area of occlusion. Under such conditions, where occlusion cannot be responsible for the disparity in retinal input, it is possible that a second strategy is implemented that favours the context consistent target. Considering that contextual cues are involved in both the integration and segregation of objects under normal viewing conditions, it is possible that contextual cues that segregate a rivalry target from its background will have a different effect from contextual cues that integrate a rivalry target with surrounding objects.

Low-level explanation: centre surround modulation

A lower-level, possibly complementary, explanation can be made by considering neuronal activity. It has been shown repeatedly that stimulus specific neuronal responses in V1 become diminished if the stimulus is embedded within an iso-oriented contextual surround, with the degree of inhibition reducing as the surrounding orientation is rotated toward orthogonal alignment.[33-36] It has similarly been shown that V1 receptive field modulation results are consistent with psychophysical data showing that orientation discrimination[36-38] and apparent contrast detection levels are reduced when the target is embedded within a 'consistent' surrounding.[39,40] If the relative level of activity of neurons corresponding to the respective rivalry target is a factor in determining perceptual dominance, one would expect that this type of receptive field modulation is having an influence on the perceptual dominance of binocular rivalry. In support of this proposal, it was reported in a very brief study by Mapperson and Lovegrove[21] that predominance of horizontal gratings over vertical gratings during binocular rivalry was successively attenuated as the background was rotated from 0°, to 5°, 10° and 20° from a vertical orientation.

As with Mapperson and Lovegrove,[21] in our experimental conditions the rivalry targets were embedded within the contextual information. Therefore, it is possible that in this circumstance there was a relative reduction in the neuronal responses corresponding to the context consistent target by the presence of the background. However, as it has been shown that this contextual suppression no longer occurs if the contextual elements are spatially separate or grouped to an independent and coherent object,[41-43] it may follow that in the Sobel and Blake experiment[13] the spatial separation of the contextual information from the target may have diminished or even reversed the effect of the context on the neuronal activity.

Phase specificity

Of no less importance than the direction of effect observed was our finding that predominance was promoted by directly increasing the dominance phase duration. This result is in line with other studies suggesting that the effect of context is unlike the majority of stimulus manipulations considered to date, which have been shown to affect the suppression phase duration. This anti-Levelt effect could reflect the role of a unique, context dependent mechanism in the resolution of interocular conflict generated during binocular rivalry. There is an equally plausible alternative explanation that puts the effect of context back in line with all other studies, showing that stimulus manipulation acts primarily on the suppression phase. The standard Levelt effect refers to the promotion of overall predominance of a 'strengthened' target through a reduction in suppression duration of that target. Conversely, the predominance of a 'weakened' target will be reduced through an increase in the suppression duration of that target. If, as was proposed in the previous paragraph, the contextual environment acts predominantly to reduce the level of neuronal activity corresponding to the context-congruent target, this would have the same effect as reducing the stimulus 'strength' of one of the rivalry targets. Therefore, the increased suppression duration of the 'weakened' context-congruent target would correspond to an increase in the dominance duration of the context-contradictory target. This brings the role of context back in line with Levelt's second proposition.

There are two main implications from this proposition that each requires further investigation through future experiments. The first is that the contextual effect reported by Sobel and Blake[13] must be mediated by an entirely different mechanism or the contextual cues generated in their stimulus effectively reduce the strength of the context-contradictory target. To our knowledge, there have been no studies that have looked explicitly at the effect of such stimuli on the level of corresponding neuronal activity. The second implication is that 'suppressability' would appear to have a disproportionately large role in determining the duration of perceptual phases in binocular rivalry.

CONCLUSION

In this study, we have shown that during binocular rivalry, contextual environment can promote the dominance of the context-contradictory target largely resulting from an increase in the dominance duration of that target. That context can have such strong, seemingly opposite effects on the rivalry process requires an explanation. It is clear that contextual information can act to increase the predominance of one of the rivalling targets but it appears that depending on the circumstances, either congruence or incongruence may be favoured. Here we have presented high level and potentially compatible low level explanations for these findings. Irrespective of the validity of our speculations, it is certain that further investigation into the intriguing effects of context will be beneficial in the attempt to better understand the neuronal processes responsible for generating the alternations in dominance and suppression that are characteristic of binocular rivalry.

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