

# Independent binocular integration for form and colour

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## Abstract

Although different features of an object are processed in anatomically distinct regions of the cerebral cortex, they often appear bound together in perception. Here, using binocular rivalry, we reveal that the awareness of form can occur independently from the awareness of colour. First, we report that, if both eyes briefly view a grating stimulus prior to the presentation of the same grating in one eye and an orthogonal grating in the other, subjects tend to report perceptual dominance of the non-primed grating. The primer was most effective when it was similar in orientation, spatial frequency and spatial phase to one of the rival images. Next, we showed that the process underlying the binocular integration of chromatic information was selectively influenced by the colour of a previously presented stimulus. We then combined these paradigms by using a primer that had the same colour as one rival stimulus, but the same form as the other stimulus. In this situation, we found that rival stimuli differing in form and colour can sometimes achieve states of dominance in which the chromatic information from one eye's image combines with the form of the other eye's image temporarily creating a binocular impression that corresponds with neither monocular component. Finally, we demonstrated that during continuous viewing of rival stimuli differing in form and colour, chromatic integration could occur independently of form rivalry. Paradoxically, however, we found that changes to the form of the stimulus had more of an influence on chromatic integration than on form rivalry. Together these phenomena show that the neural processes involved in integrating information from the two eyes can operate selectively on different stimulus features.

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## 1. Introduction

Binocular rivalry occurs when a stimulus that is clearly visible when presented to one eye, is rendered invisible when a different stimulus is presented to a corresponding region of the other eye. Despite its importance for understanding binocular vision, the neural mechanisms by which a stimulus is suppressed during rivalry remain

controversial (Alais & Blake, 2005; Andrews, 2001; Blake & Logothetis, 2002). One possibility is that visual information is suppressed by inhibitory interactions prior to the stage of monocular confluence (Blake, 1989; Lehky & Blake, 1991; Tong & Engel, 2001). In this model, interactions must occur at an early stage of visual processing such as the lateral geniculate nucleus or primary visual cortex, where neurons contain eye-of-origin information. An alternative theory is that binocular rivalry reflects selective competition between the features that comprise a stimulus (Andrews & Purves, 1997; Logothetis, Leopold, & Sheinberg, 1996). If this is the case, then, given the distributed nature of visual processing (Felleman & Van Essen, 1991; Livingstone & Hubel, 1988), it is likely that the neural events

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underlying binocular rivalry will vary according to the nature of the difference between the rival images.

Binocular rivalry can be elicited by differences in a variety of stimulus features including form, movement and colour. One approach to understand the mechanism underlying rivalry is to ask whether competition can occur independently for different stimulus features. The prediction is that, if rivalry involves a general loss of sensitivity to the image in one eye, then the dominant percept should correspond to the image in one eye. However, if rivalry involves competition between stimulus features, it should be possible for interactions between different stimulus features to occur independently. A number of studies have shown rival stimuli differing in more than one feature can generate a binocular impression that corresponds with neither monocular component (Andrews & Blakemore, 1999, 2002; Breese, 1909; Carlson & He, 2000; Carney, Shadlen, & Switkes, 1987; Cobo-Lewis, Gilroy, & Smallwood, 2000; Creed, 1935; Treisman, 1962). For example, if orthogonal grating patches moving in different directions are presented independently to each eye, one orientation can completely dominate perception, but appear to drift in a direction predicted from the combination of movements in the two eyes, implying an independent binocular interaction for form and motion (Andrews & Blakemore, 1999, 2002; Cobo-Lewis et al., 2000).

Here, we have extended this approach to ask if contour rivalry can occur independently of the binocular interaction for colour. A previous study reported that when images of different colours and forms were presented independently to the two eyes, the form of one rival image could be seen with a colour derived from both images (Breese, 1909; Creed, 1935). However, in a later experiment, using grating stimuli, Hollins and Leung (1978) stated that, ‘we have never seen a grating remain visible, but lose its colour; nor have we seen any other dissociation of stimulus properties during rivalry’. The aim of the present experiment is to use a priming paradigm to help resolve this controversy and determine whether independent processes underlie the binocular integration of form and colour. Previous studies have shown that prior viewing of a grating stimulus decreases the likelihood that it will dominate perception when viewed during binocular rivalry (Blake & Overton, 1979; Blake, Westendorf, & Overton, 1980; Ikeda & Morotomi, 2000, 2002; Pearson & Clifford, 2005; Wade & de Weert, 1986; Wolfe, 1984). In a similar way, prior viewing to a coloured patch has been shown to influence perceptual dominance during chromatic rivalry (Ikeda & Morotomi, 2000, 2002; Pearson & Clifford, 2005). Our aim is to extend these findings by defining the specific stimulus conditions that are necessary to elicit this effect and to ask whether the binocular integration of form can occur independently of that for colour.

## 2. Methods

Stimuli were programmed using a VSG2/5 graphics card (CRS, Rochester, England) and presented on Clinton Monoray or a Sony Trinitron GDM-F520 (mean luminance: 9.3 cd/m<sup>2</sup>). Both monitors had a frame-rate of 120 Hz. Gamma correction was used to ensure that the monitor was linear over the entire luminance range used in the experiments. Observers viewed the display in a darkened room at a distance of 2.28 m through ferro-electric shutter-goggles (CRS, Rochester, England), which alternately occluded the two eyes at the same frequency as the frame-rate of the monitor. Thus, successive frames were seen by only one eye with no perceptible flicker at this high alternation rate. Subjects fixated on a dark spot that remained visible throughout the experiments. In all of the experiments reported here, stimuli were circular patches with diameters measuring 1 deg. Responses were recorded via a CB3 response box (CRS, Rochester, England). All five subjects were experienced psychophysical observers and had normal or corrected-to-normal vision and good stereopsis. Subjects 1 and 2 took part in each experiment. Subject 3 took part in Experiments 1 and 4. Subject 4 only took part in Experiment 2. Subject 5 only took part in Experiment 3.

### 2.1. Experiment 1—form priming

First, we determined how a brief period of priming affects perceptual judgements of form during binocular rivalry (Fig. 1A). The primer was a circular patch of sine-wave grating that was presented to both eyes for 1 s. Immediately, following the primer, two orthogonal, sine-wave gratings (orientation,  $\pm 45$  deg; spatial frequency, 3 cycles/deg; contrast, 45%) were presented independently to corresponding regions of the left and right eye for 1 s. A counterbalanced design was used in all experiments, so that each rival stimulus was presented an equal number of times to the right and left eyes within test sessions. Subjects were then asked to report whether the left-tilted ( $-45$  deg) or right-tilted ( $+45$  deg) grating was perceptually dominant. Trials in which the subjects did not see either grating dominate perception across the whole patch and for the duration of the presentation were reported as ‘piecemeal’ rivalry. We determined the effect of changing the orientation, spatial frequency and the spatial phase of the primer across different test sessions.

### 2.2. Experiment 2—colour priming

Next, we assessed how a brief presentation of a coloured stimulus would affect the perception of two coloured stimuli presented independently to the two eyes (Fig. 1b). The priming stimulus was a circular patch of red (C.I.E. units, 0.61, 0.34), blue (C.I.E. units, 0.14, 0.07) or grey. All patches had the same luminance

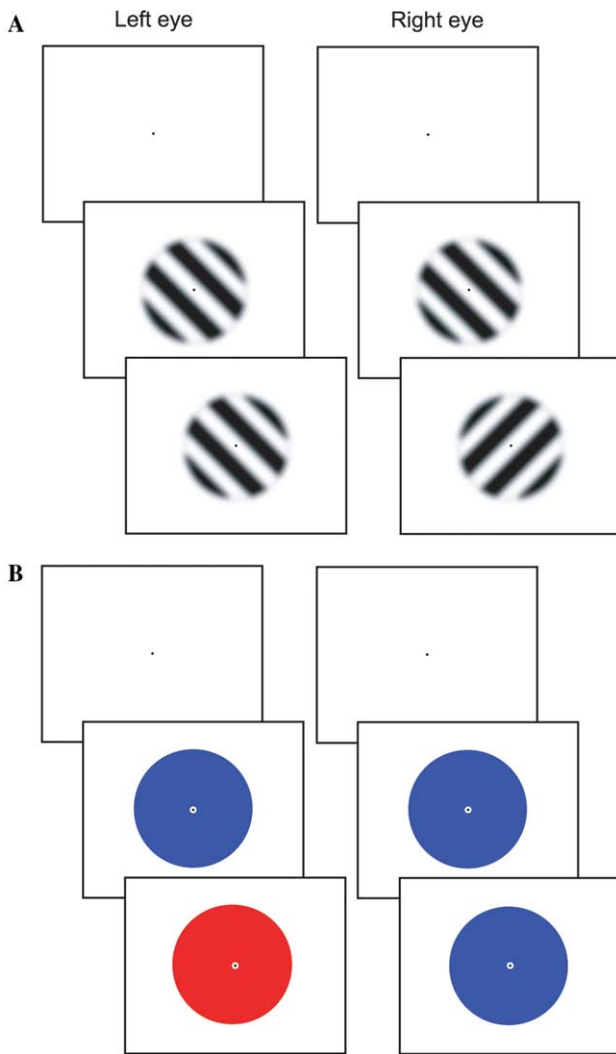


Fig. 1. Schematic showing the priming paradigm. (A) Subjects fixated a spot in the centre of the screen before viewing a grating stimulus (primer) for 1 s. The primer was followed by a left-tilted and a right-tilted grating that were presented to corresponding points in the two eyes (1 s). Subjects were asked to indicate which grating was dominant or whether piecemeal rivalry was perceived. The influence of the primer on judgments of perceptual dominance during rivalry was determined by varying the orientation, spatial frequency and spatial phase of the primer. (B) Following a period of fixation, a uniform coloured patch (primer) was presented binocularly (1 s). This was followed by the uniform red and blue patch to corresponding points in the two eyes (1 s). Subjects were asked to indicate whether the dominant percept was red, blue or fused during rivalry. We determined the effect of changing the colour of the primer on judgments of perceptual dominance during rivalry.

(6.3 cd/m<sup>2</sup>). The primer was presented to both eyes for 1 s and was followed immediately by the dichoptic presentation of two 1 deg diameter, coloured patches (one red, the other blue) to corresponding regions of the two eyes for 1 s. Subjects were asked to report their perception during the rivalry period using a 3AFC (red, blue or fused). The fused percept was typically reported as ‘purple’, and was easily distinguished from red and blue.

### 2.3. Experiment 3—form and colour priming

In this experiment, we combined the paradigms used in Experiments 1 and 2 to determine whether the binocular interactions underlying form perception could be dissociated from those underlying chromatic integration. The initial stimulus was a circular patch of grating that was presented to both eyes. The grating was achromatic and had a rectangular-wave form (duty cycle, 0.1) with an orientation of  $\pm 45$  deg and a spatial frequency of 3 cycles/deg. It was superimposed on a uniform coloured patch that was red, blue or grey (see Experiment 2). Rectangular-wave profiles were used so that the form of the grating was not defined by gradual changes in chromaticity and to maximise the amount of chromatic difference between the stimuli. The priming stimulus was presented to both eyes for 1 s. This was followed immediately by the dichoptic presentation of two stimuli that differed in both form and colour for 1 s. The rival stimuli comprised orthogonal achromatic rectangular-wave gratings (duty cycle, 0.1; orientation,  $\pm 45$  deg; spatial frequency, 3 cycles/deg) superimposed onto a uniform patch of either red or blue. Subjects were asked to report both the perception of form (left-tilted, right-tilted or piecemeal) and the perception of colour (red, blue or fused) after each trial.

### 2.4. Experiment 4—form and colour rivalry

In the final experiment, we determined whether the perception of form and colour could be dissociated during longer presentations. The stimuli were patches of achromatic rectangular-wave grating (duty cycle, 0.3; spatial frequency, 3 cycles/deg) superimposed on a uniform blue or red background. The angular difference between the gratings was varied from 22.5 deg to 90 deg in different trials. Subjects fixated a dark spot in the centre of the screen during each 2 min trial and pressed one of three keys to indicate changes in either form (orientation) or colour in alternate trials. During the form trials, subjects only indicated dominance of the left-tilted grating, the right-tilted grating or piecemeal rivalry. During the colour trials, subjects only reported perceptual dominance of red, blue or fused (‘purple’). It is important to note that the chromatic differences do not exist at the intersections between the achromatic gratings.

## 3. Results

### 3.1. Experiment 1—form priming

Subjects viewed an identical grating stimulus (primer) in both eyes prior to the dichoptic presentation of a left-tilted and a right-tilted oblique grating on corresponding

regions of the two eyes. If the primer had an orientation that was the same or similar to one of the dichoptically presented gratings, subjects were most likely to report dominance of the other, non-primed grating during the rivalry period (Fig. 2). For example, when the orientation of the primer grating was tilted to the right (+45 deg), subjects reported dominance of the left-tilted grating (−45 deg) during rivalry on over 80% of presentations (mean  $\pm$  SEM =  $85 \pm 5$ ). As the primer was gradually changed to being left-tilted (−45 deg), perception switched toward the right-tilted grating (+45 deg) during the rivalry period. An ANOVA shows that the effect of orientation on perceptual dominance was significant in all subjects (S1:  $F(10, 40) = 81.49$ ,  $p < .001$ ; S2:  $F(10, 40) = 35.40$ ,  $p < .001$ ; S3:  $F(10, 40) = 35.67$ ,  $p < .001$ ).

Next, we determined whether the effect of the primer was selective for spatial frequency (Fig. 3). As the spatial frequency of the primer grating was made progressively different from that of the rival gratings, its ability to influence perceptual judgments during rivalry diminished. For example, if the primer had the same spatial

frequency (3 cycles/deg) and orientation as one of the dichoptically presented gratings, subjects reported that the non-primed grating was dominant during the rivalry period on over 80% of trials (mean  $\pm$  SEM =  $84 \pm 6$ ). However, as the spatial frequency of the primer grating was increased or decreased, its influence on which rival stimulus was perceptually dominant during binocular rivalry was gradually reduced. An ANOVA revealed that the effect of spatial frequency was significant for all subjects (S1:  $F(6, 24) = 22.76$ ,  $p < .001$ ; S2:  $F(6, 24) = 10.40$ ,  $p < .001$ ; S3:  $F(6, 24) = 20.44$ ,  $p < .001$ ).

Finally, we examined the effect of changing the spatial phase of the priming stimulus (Fig. 4). The effect of the primer was greatest when it had a similar spatial phase, spatial frequency and orientation as one of the dichoptically presented gratings. However, as the spatial phase of the primer grating was changed, its influence on which grating was perceptually dominant during binocular rivalry gradually diminished. An ANOVA showed that the effect of spatial phase was significant in all subjects (S1:  $F(7, 28) = 29.14$ ,  $p < .001$ ; S2:  $F(7, 28) = 11.45$ ,  $p < .001$ ; S3:  $F(7, 28) = 5.72$ ,  $p < .001$ ).

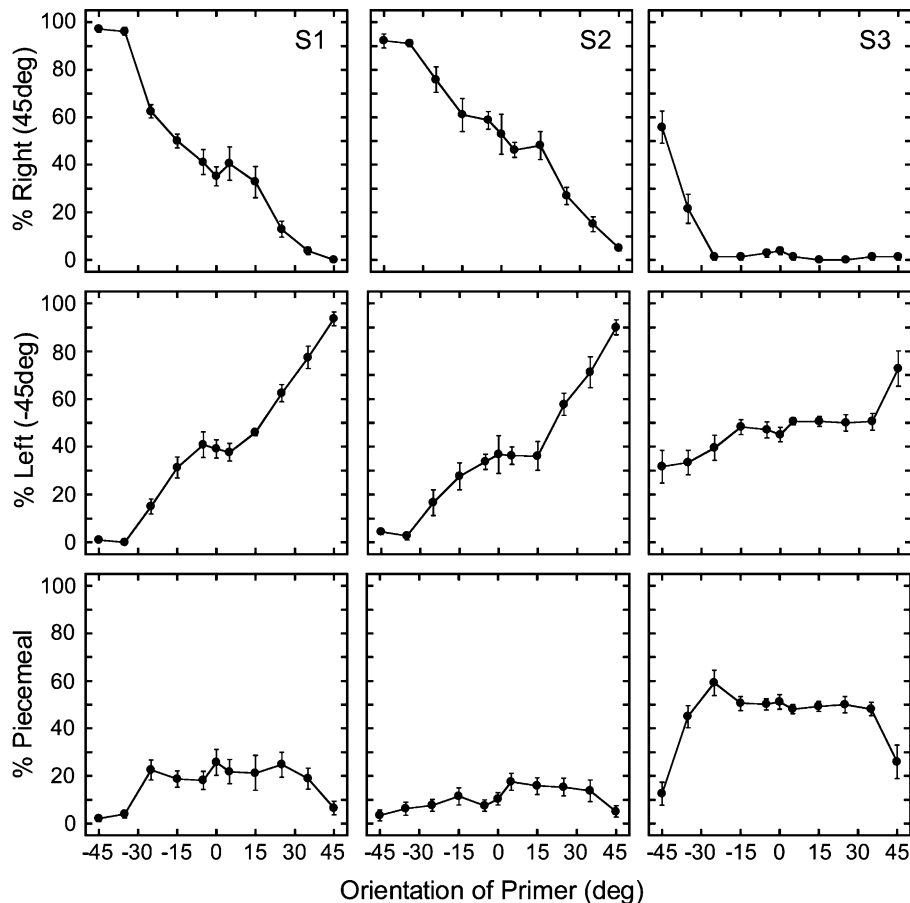


Fig. 2. The effect of changing the orientation of the primer grating on perceptual judgments during contour rivalry. The graphs show the proportion of trials in which either the left-tilted grating, the right-tilted grating or piecemeal rivalry were reported. The symbols and error bars represent the mean and SEM from 80 trials.

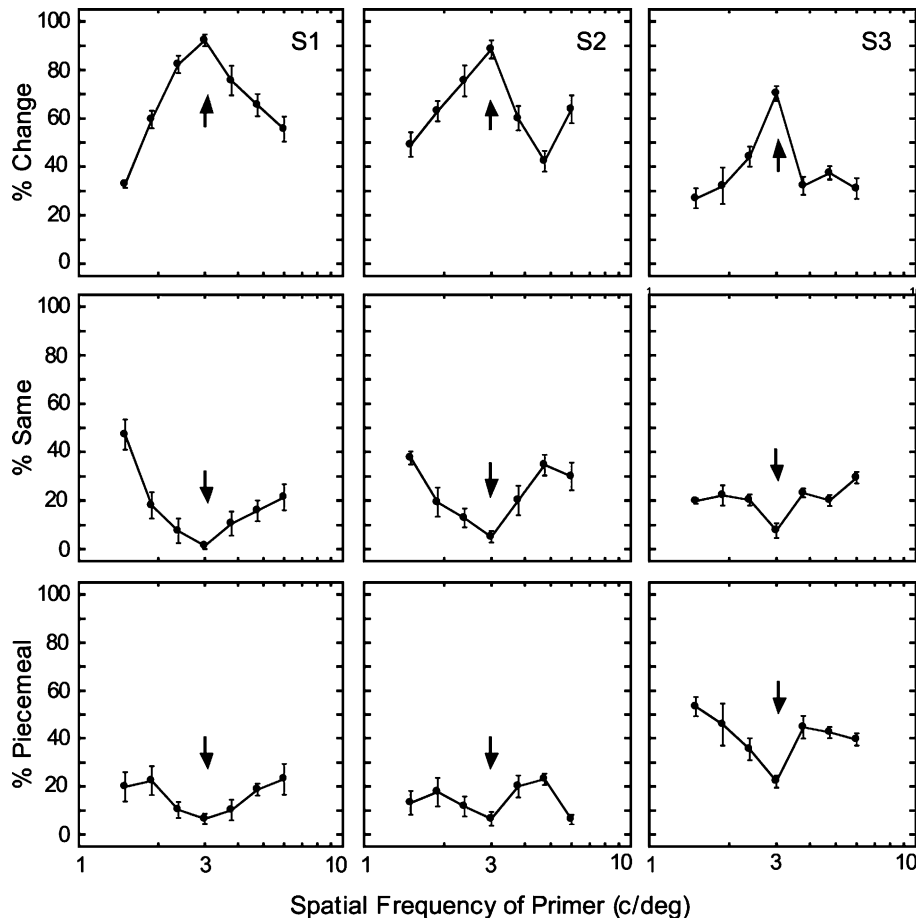


Fig. 3. The effect of changing the spatial frequency of the primer on perceptual judgments during binocular rivalry. The primer had the same orientation of one of the rival gratings. The graphs show the proportion of trials in which the orientation of the dominant grating during rivalry was the same or different to the primer. The arrow indicates the spatial frequency of the rival gratings. Trials in which neither grating was fully dominant were reported as piecemeal. The symbols and error bars represent the mean and SEM from 80 trials.

### 3.2. Experiment 2—colour priming

In this experiment, we determined how the presentation of a uniform coloured patch (primer) to both eyes would affect the subsequent perception of two dichoptically presented coloured patches (one red, one blue) (Fig. 5). When the primer was red, subjects reported dominance of the blue patch during rivalry in over 75% of trials (mean  $\pm$  SEM =  $78 \pm 8$ ), a fused percept on about 20% of trials (mean  $\pm$  SEM =  $22 \pm 7$ ) and dominance of the red patch in less than 1% of trials (mean  $\pm$  SEM =  $0.6 \pm 0.1$ ). In contrast, if the priming stimulus was blue, subjects reported dominance of the red stimulus in over 65% of trials (mean  $\pm$  SEM =  $66 \pm 14$ ), a fused percept on about 30% of trials (mean  $\pm$  SEM =  $33 \pm 14$ ) and dominance of the blue patch in less than 1% of trials (mean  $\pm$  SEM =  $0.5 \pm 0.4$ ). When the priming patch had a neutral colour (grey), subjects reported a fused percept (neither blue nor red) in 85% of trials (mean  $\pm$  SEM =  $85 \pm 11$ ). An ANOVA showed that the colour of the primer had a significant effect on

which stimulus was dominant during binocular rivalry (S1:  $F(2,8) = 807.54$ ,  $p < .001$ ; S2:  $F(2,8) = 48.28$ ,  $p < .001$ ; S4:  $F(2,8) = 150.70$ ,  $p < .001$ ).

### 3.3. Experiment 3—form and colour priming

We combined the paradigms used in Experiments 1 and 2, to determine if the binocular processes underlying the integration of colour and form were independent. When the primer had the same orientation and colour as one of the rival stimuli, subjects reported perceptual dominance of the form and colour from the non-primed grating in 75% (mean  $\pm$  SEM =  $75 \pm 12$ ) of trials (Fig. 6). In other words, at the onset of rivalry, the dominant perception of colour and form was congruent with the stimulus in one eye. In about 10% of trials (mean  $\pm$  SEM =  $11 \pm 5$ ), subjects reported that a fused colour coexisted with total dominance of the form from one eye or the other. In less than 3% of trials (mean  $\pm$  SEM =  $2.7 \pm 1$ ), subjects reported the incongruent perception of the form from one eye and the colour from the other.



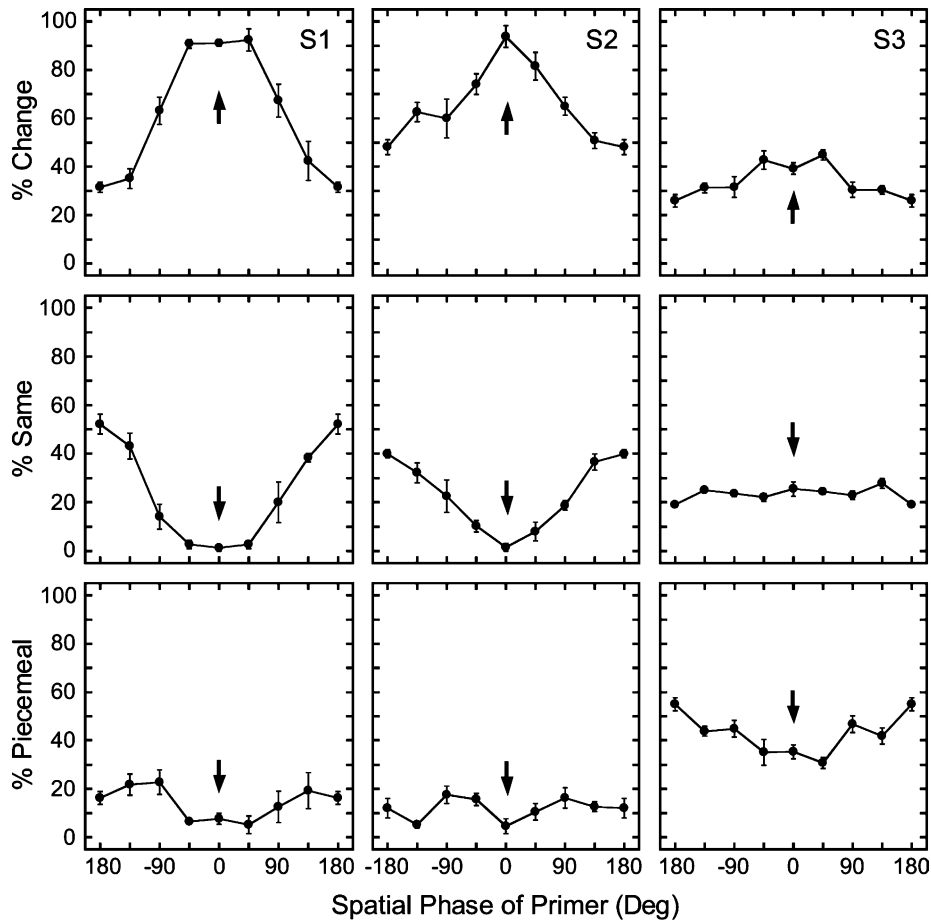


Fig. 4. The effect of changing the spatial phase of the primer on perceptual reports during binocular rivalry. The primer had the same orientation as one of the rival gratings. The graphs show the proportion of trials in which the dominant orientation during rivalry was the same or different to that of the primer. The arrow indicates the spatial phase of the rival gratings. Trials in which neither grating was fully dominant are reported as piecemeal. The symbols and error bars represent the mean and SEM from 80 trials.

Next, we used a primer that had the same form (orientation) as one of the rival stimuli, but was superimposed on a neutral (achromatic) patch (Fig. 7). In this condition, subjects reported a change in perceptual dominance to the non-primed form on about 60% of trials (mean  $\pm$  SEM =  $59 \pm 9$ ). However, on over 60% of these trials (mean  $\pm$  SEM =  $67 \pm 12$ ), subjects reported that the perceived colour of the stimulus was a fusion between the two rival stimuli. In less than 1% of trials (mean  $\pm$  SEM =  $0.5 \pm 0.1$ ), subjects reported the incongruent perception of the form from one eye and the colour from the other.

Finally, we determined how a primer with the form (orientation) from one rival stimulus, but the colour from the other would affect perceptual judgements during rivalry (Fig. 8). On about 30% of trials (mean  $\pm$  SEM =  $30 \pm 7$ ), subjects reported the congruent perceptual dominance of the form and colour from one eye's stimulus. However, on over 30% of trials (mean  $\pm$  SEM =  $38 \pm 5$ ) subjects reported that the form from one image dominated perception, but that the perceived colour of the stimulus was a fusion between the two

images. Finally, on 15% of trials (mean  $\pm$  SEM =  $15 \pm 5$ ), subjects reported the incongruent perception of the form from one eye and the colour from the other.

#### 3.4. Experiment 4—form and colour rivalry

In this experiment, we asked whether the perception of form and colour could be dissociated during the ongoing alternations in dominance that accompany longer periods of binocular rivalry (Fig. 9). Overall, subjects reported more alternations in form than colour (S1:  $F(1,7) = 104.4$ ,  $p < .001$ ; S2:  $F(1,7) = 38.51$ ,  $p < .001$ ; S3:  $F(1,7) = 20.29$ ,  $p < 0.05$ ). Interestingly, changing the angular difference between the two gratings had a different effect on the number of alternations perceived during the form and colour trials. Paradoxically, an interaction reveals that changing the difference in form between the two stimuli had a more marked influence on alternations in colour compared to form (S1:  $F(3,21) = 4.80$ ,  $p < .05$ ; S2:  $F(3,21) = 5.67$ ,  $p < .01$ ; S3:  $F(3,21) = 5.15$ ,  $p < .01$ ).

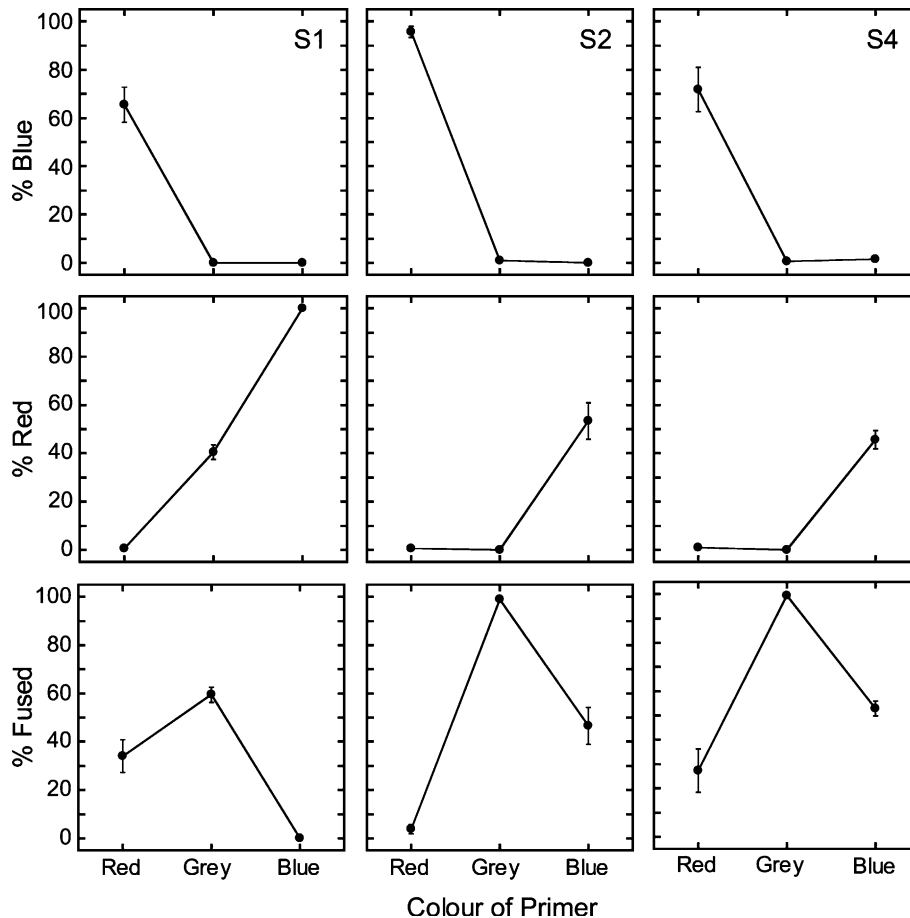


Fig. 5. The effect of changing the colour of the primer on perceptual reports during colour rivalry. The graphs show the proportion of trials in which the dominant perception was red, blue or a fusion of the two colours. The symbols and error bars represent the mean and SEM from 80 trials.

The period of total dominance was greater for form compared to colour (S1:  $F(1,7) = 357.1$ ,  $p < .001$ ; S2:  $F(1,7) = 378.5$ ,  $p < .001$ ; S3:  $F(1,7) = 17.9$ ,  $p < .01$ ). Furthermore, increasing the angular difference between the two gratings had a differential effect on total dominance reports for colour versus form. When the difference between the two gratings was small (22.5 deg), subjects reported complete dominance of one colour or the other for about 20% of the viewing period (mean  $\pm$  SEM =  $23.6 \pm 2.1$ ); the same stimulus conditions resulted in total dominance of one form or the other for over 80% of the viewing period (mean  $\pm$  SEM =  $81.2 \pm 11.7$ ). However, when the angular difference between gratings was increased (90 deg), subjects reported total dominance of one or the other colour for about 70% of the viewing period (mean  $\pm$  SEM =  $67.4 \pm 12.9$ ); total dominance of one form or the other remained at about 80% of the viewing period (mean  $\pm$  SEM =  $81.1 \pm 17.4$ ). The increase in the total dominance for colour was matched by a decrease in the proportion of the viewing time that subjects reported fusion of the two colours. An interaction revealed a significant difference in the effect of angular difference on total dominance for col-

our and form in two of the three subjects ( $F(3,21) = 17.73$ ,  $p < .05$ ;  $F(3,21) = 56.13$ ,  $p < .001$ ;  $F(3,21) = 1.78$ ,  $p = .18$ ).

#### 4. Discussion

Our aim in this study was to determine whether the processes underlying the binocular integration of form and colour are independent. We report that rival stimuli differing in form and colour can sometimes achieve states of dominance in which the chromatic information from one eye's image combines with the form of the other eye's image temporarily creating a binocular impression that corresponds with neither monocular component.

First, we found that if both eyes briefly view a grating prior to the presentation of the same grating in one eye and a different grating in the other, subjects regularly report perceptual dominance of the novel, non-primed grating. This finding confirms previous reports showing that adaptation to a grating decreases the likelihood of its dominance during binocular rivalry (Blake

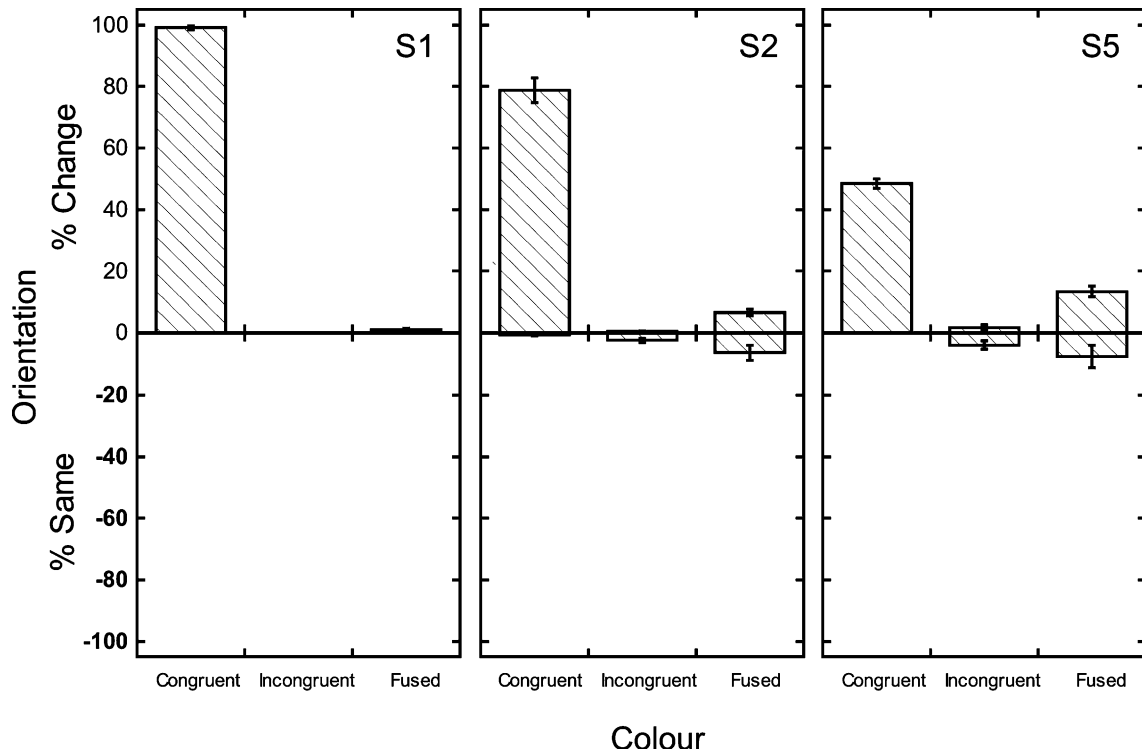


Fig. 6. The effect of a primer with the same form (orientation) and colour as one of two rival stimuli. The y-axis on the graphs shows the proportion of trials in which the dominant form (orientation) was the same as or different to that of the primer stimulus. The x-axis shows the proportion of trials in which the dominant colour was congruent or incongruent with form from one stimulus, or was a fusion of the two colours (fused). Less than 5% of trials contained piecemeal rivalry (data not shown). The columns and error bars represent the mean and SEM from 80 trials.

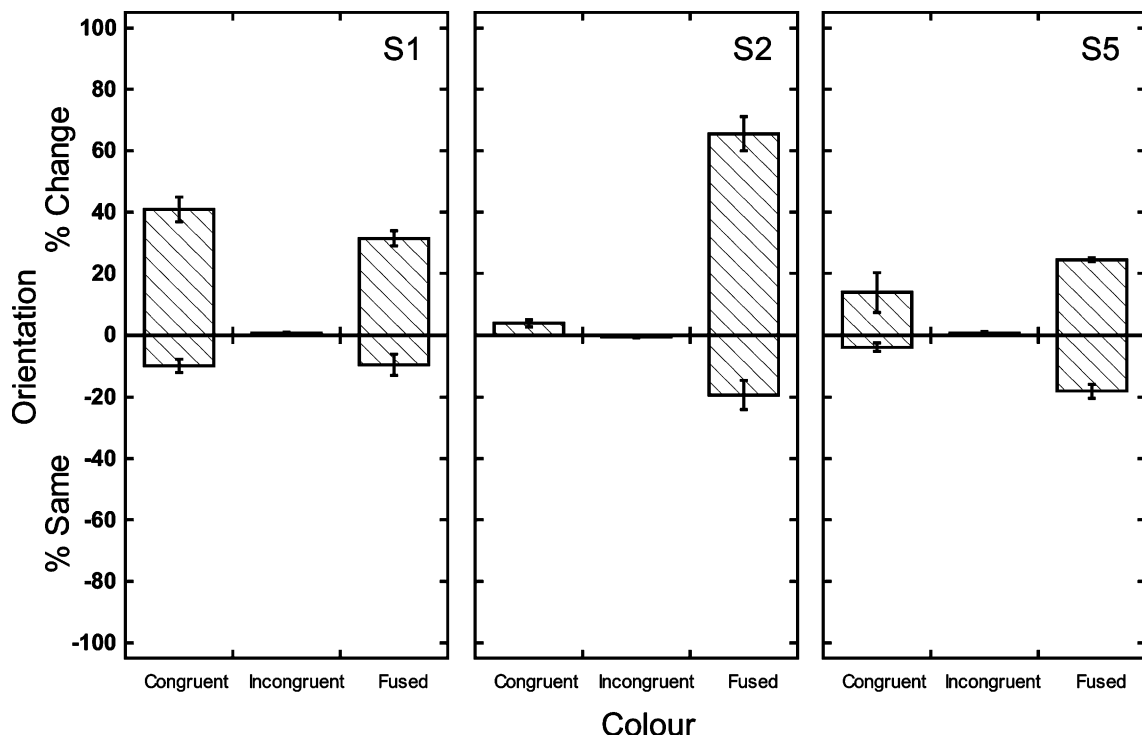


Fig. 7. The effect of a primer with the same form (orientation) as one of two rival stimuli, but a neutral colour. The y-axis on the graphs shows the proportion of trials in which the dominant form (orientation) was the same as or different to that of the primer. The x-axis shows the proportion of trials in which subjects reported the dominant colour as red, blue or a fusion of the two colours. Less than 10% of trials contained piecemeal rivalry (data not shown). The columns and error bars represent the mean and SEM from 80 trials.



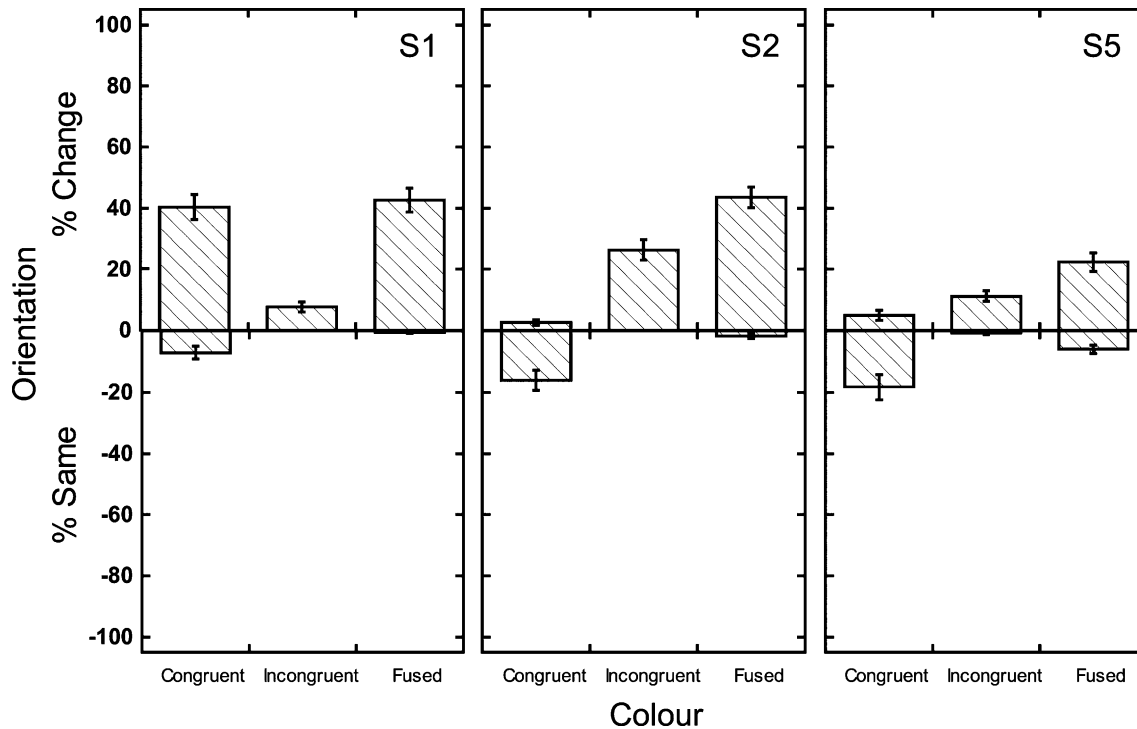


Fig. 8. The effect of a primer with the same form (orientation) as one rival stimulus, but the same colour as the other stimulus. The y-axis on the graphs shows the proportion of trials in which the dominant form (orientation) was the same as or different to that of the primer. The x-axis shows the proportion of trials in which the dominant colour was congruent or incongruent with form from one stimulus, or was a fusion of the two colours (fused). Less than 10% of trials contained piecemeal rivalry (data not shown). The columns and error bars represent the means and SEM from 80 trials.

& Overton, 1979; Blake et al., 1980; Ikeda & Morotomi, 2000; Pearson & Clifford, 2005; Wade & de Weert, 1986). However, we extend these findings by showing that the influence of the priming grating was only apparent if the orientation, spatial frequency and spatial phase were similar to one of the rival stimuli. The sensitivity to particular characteristics of the primer suggests that the initial selection for dominance during binocular rivalry involves neurons that are tuned for specific features of the stimulus (DeValois, Yund, & Hepler, 1982; Hubel & Wiesel, 1968). Consistent with this conclusion, a number of studies have shown the temporal dynamics of binocular rivalry can be influenced by changing different aspects of the rival stimuli such as spatial frequency and orientation (Andrews & Purves, 1997; Breese, 1909; Levelt, 1968; O'Shea, Sims, & Govan, 1997; Yang, Rose, & Blake, 1992). However, because the rival images were presented immediately after the primer, it is also possible that the results could be explained by the relative amount of transient signal in the two eyes. When the primer was the same as one of the rival images, the image in one eye was changed but the image in the other eye remained the same. Thus, there was a transient signal in one eye, but not in the other. As the primer was made more different from one of the two gratings the relative amount of transient signal decreased, making

it less likely that the non-primed grating would be dominant.

Next, we asked whether priming could also influence perceptual dominance during chromatic rivalry. Our results show that the mechanism underlying the binocular integration of chromatic information was selectively influenced by the colour of a previously presented stimulus (see also, Ikeda & Morotomi, 2000, 2002). For example, when a blue patch was shown to both eyes prior to viewing a blue patch in one eye and a red patch in a corresponding location of the other eye, subjects frequently reported dominance of the non-primed red patch. In contrast, when the primer was a red patch, the dominant stimulus during rivalry was the blue patch. Finally, when subjects viewed a neutral grey primer, perception during rivalry was predominantly of a fused colour. It is interesting to note the difference between form and colour rivalry when the priming stimulus is not biased toward either rival stimulus. In this instance, form signals tend to rival, whereas colour signals tend to fuse. A similar dissociation is apparent when stimuli differing in form and motion are presented independently to the two eyes; the motion signals can fuse, while form signals continue to compete for perceptual dominance (Andrews & Blake, 1999, 2002; see also Carney et al., 1987).

We then combined the form and colour priming paradigms to probe the independence of the processes

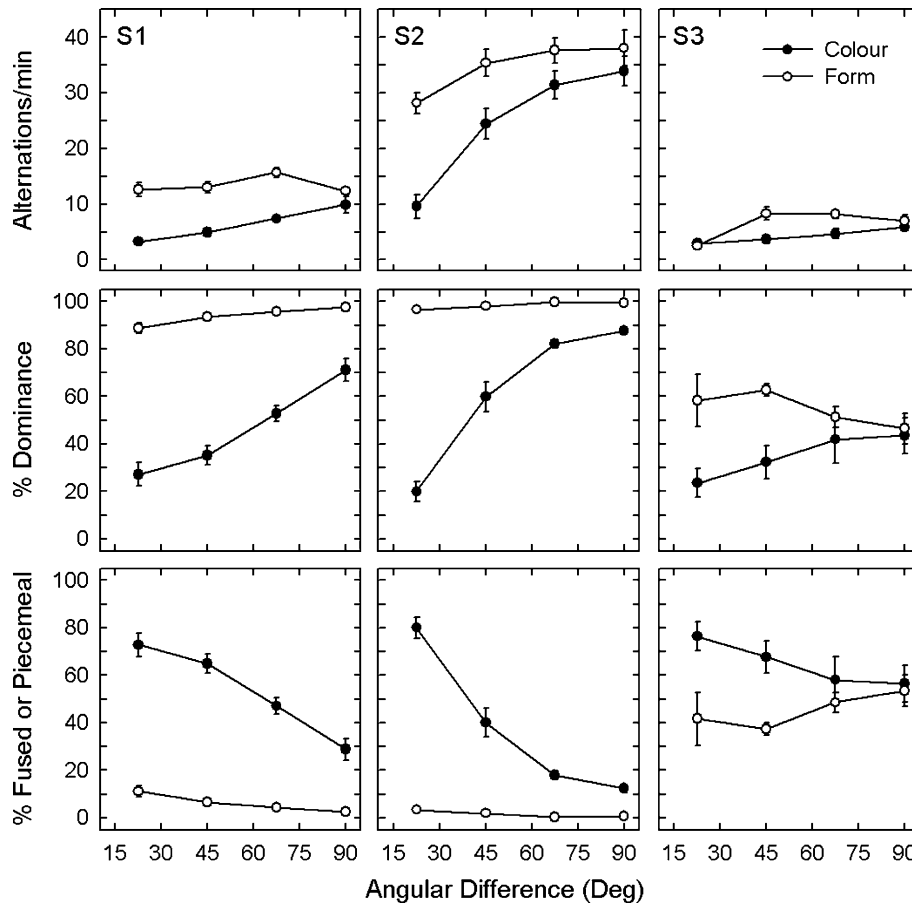


Fig. 9. Summary of perceptual reports when viewing two rival stimuli that differed in form and colour. Subjects reported changes in the form or colour of the stimulus during 2 min trials. The angular difference between gratings was varied between trials. Each symbol and error bar represents the mean and SEM from eight trials.

underlying binocular integration. Specifically, we determined the effect of a primer that had the same chromatic background as one rival stimulus, but the form of the other. The results show that on some trials (~30%) the dominant form and colour were congruent with the stimulus presented to one eye. However, on a similar number of the trials (~30%), the colour information from the two eyes combined, while the form from one eye dominated perception. Finally, on other trials (15%) subjects reported that the dominant perception included an illusory conjunction of the form from one eye, but the colour from the other. The implication of this experiment is that the binocular integration of form and colour information can occur independently.

In the final experiment, we determined whether the binocular integration of form and chromatic information could occur independently during longer viewing periods. Creed (1935) reported that when images of different colours and forms were presented independently to the two eyes, colour fusion occurred simultaneously with the dominance of the form from one eye. However, Hollins and Leung (1978) later claimed never to have seen an independent interaction for form and colour.

Our findings offer a clear explanation for this disagreement, by showing that the amount of chromatic fusion was influenced by the angular difference in the gratings presented to each eye. When the angular difference between the gratings is small, colour fusion is the dominant perception. Despite the prevailing colour fusion, the same stimulus conditions give rise to total dominance of the form from one eye or the other. However, when the angular difference is large (i.e., the gratings are orthogonal) the proportion of the viewing period in which the colours appear fused declines and the dominant perception is total dominance of the colour from one eye or the other. In this situation, the alternations in colour dominance were very similar to the alternations in form. The stamps used by Creed (1935) had designs that on average would have small angular differences compared with the orthogonal gratings used by Hollins and Leung (1978). Based on our findings, the stamps would be expected to produce less colour dominance (more colour fusion) than orthogonal grating stimuli. This interpretation is also consistent with a study from DeWeert and Wade (1988), who showed that dichoptic colour fusion is more apparent when

identical forms are superimposed on the images in the two eyes.

Although these results imply independent processing of colour and form, it is interesting to note that changes in the form of the two rival stimuli had a greater influence on the binocular integration of chromatic information than on form, indicating some interaction between these stimulus features. Physiological studies have found that oriented neurons in visual cortex can be selective for wavelength, as well as luminance (Engel, 2005; Johnson, Hawken, & Shapley, 2001; Schluppeck & Engel, 2002). Presumably, interactions between these neurons could explain the influence of form on colour during binocular rivalry. However, the binocular interactions underlying chromatic integration are known to be based on the perception of surface appearance rather than on the particular wavelength received by the eye (Andrews & Lotto, 2004; see also Wallach & Adams, 1954). This would imply that the binocular interactions underlying colour also involve area V4/V8. This is because activity in this area can be correlated with sensations of surface colour independent of changes in illumination (Schein & Desimone, 1990; Zeki, 1983) and lesions to this region of visual cortex often result in a deficit in the ability to perceive and discriminate colour (Heywood, Cowey, & Newcombe, 1991). However, a recent report has suggested that perceived colour could be represented by neurons in the primary visual cortex (Wachtler et al., 2003). Consequently, it may be that the neural processes that underlie the binocular integration of chromatic information do not reduce to any one area, but represent a distributed pattern of neural events that emerge from interactions between cortical areas.

Can we draw any conclusions about where the binocular interactions involving form might occur? Most neurons in primary visual cortex respond selectively to bars and gratings at particular orientations (DeValois et al., 1982; Hubel & Wiesel, 1968). Although, these neurons exhibit significant interocular suppression during contour rivalry (Sengpiel & Blakemore, 1994; Sengpiel, Blakemore, & Harrad, 1995), single unit studies report that only a small proportion of such neurons display fluctuations in activity that co-varies with shifts in perceptual dominance (Leopold & Logothetis, 1996). It is only in extrastriate visual areas, particularly within the temporal lobe, that a greater proportion of neurons show activity that follow the ongoing perceptual alternations observed during binocular rivalry (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Although these results are consistent with the idea that rivalry involves neuronal competition in extrastriate cortex, a number of recent brain imaging studies have reported that activity in primary visual cortex covaries with changes in perception occurring during contour rivalry (Lee, Blake, & Heeger, 2005; Polonsky, Blake, Braun,

& Heeger, 2000; Tong & Engel, 2001). Thus, it is possible that the binocular interactions underlying form processing may also result from a distributed pattern of neural events.

Although the findings from this and other studies (Andrews & Purves, 1997; Kovacs, Pappathomas, Yang, & Feher, 1996; Logothetis et al., 1996) support the idea that selective interactions between stimulus features are responsible for binocular rivalry, this conclusion is challenged by other studies that reveal a more non-selective competition between the eyes. For example, during binocular rivalry observers often fail to notice large changes in the spatial frequency or orientation of a suppressed grating (Blake & Lema, 1978; Blake & Fox, 1974). The non-specific nature of suppression has been taken as evidence that rivalry involves competition between the 'eyes' (monocular channels) rather than between different stimulus features (Blake, 1989). Other evidence in support of this idea is apparent in studies in which the images in the two eyes are switched during binocular rivalry. For most stimulus conditions this causes an immediate switch in perception from the dominant to the non-dominant stimulus (Blake et al., 1980; Lee & Blake, 1999; although see Logothetis et al., 1996); if stimulus features were competing for perceptual dominance, the prediction would be that the dominant perception should remain unchanged. Based on this evidence, it would appear that a region of one eye is dominant rather than a given stimulus.

A possible explanation for the discrepancy about what competes for perceptual dominance could be that binocular rivalry does not involve a single neural mechanism (Blake, 1989). Rather the neural processes that underlie binocular rivalry occur at multiple stages of visual processing (Alais & Blake, 2005; Blake & Logothetis, 2002; Blake, 2001). Logically, the visual system must first determine whether the images in the two eyes should fuse or rival. Given the parallel nature of visual processing, it is likely that this registration process will vary with the type of image in the two eyes and involve interactions between neurons that are tuned to specific features of the stimulus. If having determined that the images are incompatible, the visual system must then have a mechanism to suppress one monocular image and render the other dominant. It is quite conceivable that this process could involve feedback to neurons in early visual areas that contain eye of origin information (Watson, Pearson, & Clifford, 2004; Wilson, 2003).

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## References

- Alais, D., & Blake, R. (2005). *Binocular rivalry*. Cambridge, MA: MIT.
- Andrews, T. J. (2001). Binocular rivalry and visual awareness. *Trends in Cognitive Sciences*, 10, 407–409.
- Andrews, T. J., & Blakemore, C. (1999). Form and motion have independent access to conscious perception. *Nature Neuroscience*, 2, 405–406.
- Andrews, T. J., & Purves, D. (1997). Similarities in normal and binocularly rivalrous viewing. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 9905–9908.
- Andrews, T. J., & Blakemore, C. (2002). Integration of motion information during binocular rivalry. *Vision Research*, 42, 301–309.
- Andrews, T. J., & Lotto, R. B. (2004). Fusion and rivalry are based on the perceptual meaning of visual stimuli. *Current Biology*, 14, 418–423.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96, 145–167.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3, 1–11.
- Blake, R. (2001). Primer on binocular rivalry, including controversial issues. *Brain and Mind*, 2, 5–38.
- Blake, R., & Lema, S. A. (1978). Inhibitory effect of binocular rivalry suppression is independent of orientation. *Vision Research*, 18, 541–544.
- Blake, R., & Fox, R. (1974). Binocular rivalry suppression: Insensitive to spatial frequency and orientation change. *Vision Research*, 14, 687–692.
- Blake, R., & Overton, R. (1979). The site of binocular rivalry suppression. *Perception*, 8, 143–152.
- Blake, R., Westendorf, D. H., & Overton, R. (1980). What is suppressed during binocular rivalry? *Perception*, 9, 223–231.
- Breese, B. B. (1909). Binocular rivalry. *Psychological Review*, 16, 410–415.
- Carlson, T. A., & He, S. (2000). Visible binocular beats from invisible stimuli during rivalry. *Current Biology*, 10, 1055–1058.
- Carney, T., Shadlen, M., & Switkes, E. (1987). Parallel processing of motion and colour information. *Nature*, 328, 647–649.
- Cobo-Lewis, A. B., Gilroy, L. A., & Smallwood, T. B. (2000). Dichoptic plaids may rival, but their motions can integrate. *Spatial Vision*, 13, 415–429.
- Creed, R. S. (1935). Observations on binocular fusion and rivalry. *Journal of Physiology*, 84, 381–392.
- DeValois, R. L., Yund, E. W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, 22, 531–544.
- DeWeert, C. M., & Wade, N. J. (1988). Compound binocular rivalry. *Vision Research*, 28, 1031–1040.
- Engel, S. A. (2005). Adaptation of oriented and unoriented color-selective neurons in human visual areas. *Neuron*, 45, 613–623.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1–47.
- Heywood, C. A., Cowey, A., & Newcombe, F. (1991). Chromatic discrimination in a cortically color blind observer. *European Journal of Neuroscience*, 3, 802–812.
- Hollins, M., & Leung, E. H. L. (1978). The influence of colour on binocular rivalry. In J. Armington, J. Krauskopf, & B. R. Wooten (Eds.), *Visual psychophysics and physiology* (pp. 181–190). New York: Academic Press.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of macaque visual cortex. *Journal of Physiology*, 195, 215–243.
- Ikeda, K., & Morotomi, T. (2000). Feature-specific priming effects upon short duration binocular rivalry. *Psychologia*, 43, 123–134.
- Ikeda, K., & Morotomi, T. (2002). Color-specific filtering of rival binocular inputs induced by priming? *Japanese Psychological Research*, 44, 57–65.
- Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience*, 4, 409–416.
- Kovacs, I., Papathomas, T. V., Yang, M., & Feher, A. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 15508–15511.
- Lee, S. H., & Blake, R. (1999). Rival ideas about binocular rivalry. *Vision Research*, 39, 1447–1454.
- Lee, S. H., Blake, R., & Heeger, D. J. (2005). Traveling waves of activity in primary visual cortex during binocular rivalry. *Nature Neuroscience*, 8, 22–23.
- Lehky, S. R., & Blake, R. (1991). Organization of binocular pathways: Modeling and data related to rivalry. *Neural Computation*, 3, 44–53.
- Levelt, W. (1968). *On binocular rivalry*. Stoesterberg, The Netherlands: Institute for Perception RVOTNO.
- Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkey's percepts during binocular rivalry. *Nature*, 379, 549–553.
- Livingston, M., & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240, 740–749.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivaling during binocular rivalry? *Nature*, 380, 621–624.
- O'Shea, R. P., Sims, A. J. H., & Govan, D. G. (1997). The effect of spatial frequency and field size on the spread of exclusive visibility in binocular rivalry. *Vision Research*, 37, 175–183.
- Pearson, J., & Clifford, C. W. G. (2005). Mechanisms selectively engaged in rivalry: Normal vision habituates, rivalrous vision primes. *Vision Research*, 42, 707–714.
- Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience*, 3, 1153.
- Schein, S. J., & Desimone, R. (1990). Spectral properties of V4 neurons in the Macaque. *Journal of Neuroscience*, 10, 3369–3389.
- Schluppeck, D., & Engel, S. A. (2002). Color opponent neurons in V1: A review and model reconciling results from imaging and single-unit recording. *Journal of Vision*, 2, 480–492.
- Sengpiel, F., & Blakemore, C. (1994). Interocular control of neuronal responsiveness in cat visual cortex. *Nature*, 368, 847–850.
- Sengpiel, F., Blakemore, C., & Harrad, R. (1995). Interocular suppression in primary visual cortex: A possible neural basis of binocular rivalry. *Vision Research*, 35, 179–195.
- Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organisation. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 3408–3413.
- Tong, F., Nakayama, K., Vaughan, J., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, 21, 753–759.
- Tong, F., & Engel, S. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, 411, 195–199.
- Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. *Quarterly Journal of Experimental Psychology*, 14, 23–29.
- Wade, N. J., & de Weert, C. M. M. (1986). Aftereffects in binocular rivalry. *Perception*, 15, 419–434.
- Wallach, H., & Adams, P. A. (1954). Binocular rivalry of achromatic colors. *American Journal of Psychology*, 67, 513–516.
- Watson, T. L., Pearson, J., & Clifford, C. W. G. (2004). Perceptual grouping of biological motion promotes binocular rivalry. *Current Biology*, 14, 1670–1674.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 14499–14503.
- Wolfe (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research*, 24, 471–478.

Yang, Y., Rose, D., & Blake, R. (1992). On the variety of percepts associated with dichoptic viewing of dissimilar monocular stimuli. *Perception, 21*, 47–62.

Zeki, S. (1983). Colour coding in the cerebral cortex: The responses of cells in monkey visual cortex to wavelengths and colours. *Neuroscience, 9*, 741–756.