5. Eye Suppression and Feature Suppression

Summary

Binocular rivalry involves two incompatible stimuli and competition between opposing percepts: one stimulus is seen and the other is suppressed. There are two hypotheses, *eye suppression* and *feature suppression*, about the cortical site of suppression. The former claims that monocular channels in the visual system alternate between dominance and suppression, while the latter assumes that the suppression acts on stimulus features encoded by binocular cells in high-level cortex. This chapter aimed to compare these two hypotheses by using a brief test stimulus, delivered to one or both eyes, and similar in features to one or the other rivalry-inducing stimulus. The results matched the predictions of the eye suppression but not the feature suppression hypothesis. It is concluded that feature suppression cannot occur without eye suppression, which is a necessary condition for binocular rivalry. Binocular rivalry is therefore initiated in the only cortical area containing significant numbers of monocularly-driven cells, the primary visual cortex, or in the structure that provides its input.

Introduction

The study of rivalry has been accompanied by a controversy about the location in the visual pathway at which the suppressive effects of rivalry are exerted. Logothetis, Leopold & Sheinberg (1996) described two hypotheses for the origin of the loss of visibility during binocular rivalry suppression. Eye suppression is exerted indiscriminately on any stimulus presented to the suppressed eye. It is assumed to act on monocularly-driven cortical cells, and has its effect in the primary visual cortex. Feature suppression (termed stimulus rivalry by Logothetis et al.) affects a stimulus feature regardless of which eye views the
feature. It is assumed to act on binocular cells and therefore resides beyond the level of eye suppression.

The eye suppression hypothesis is backed up by psychophysical evidence (Blake, Westendorf & Overton, 1980; Nguyen, Freeman & Wenderoth, 2001) and by functional magnetic resonance imaging on humans showing activity modulation in a monocularly-driven cortical area (Tong & Engel, 2001). Very recently there have also been reports that rivalry modulates activity in the lateral geniculate nucleus (Haynes, Deichmann & Rees, 2005; Wunderlich, Schneider & Kastner, 2005). The feature suppression hypothesis is supported by the finding of normal rivalrous alternation when the stimuli are switched rapidly between eyes (Logothetis et al., 1996), by the correlation of responses in higher cortical neurons with perception (Sheinberg & Logothetis, 1997), and by imaging of high-order cortical areas during rivalry (Tong, Nakayama, Vaughan & Kanwisher, 1998). There appears to be no direct comparison of the two hypotheses in the literature: how can they be simply compared? This chapter describes an experiment designed to answer this question. First, binocular rivalry was induced and the visual loss during suppression measured. Second, a test stimulus was delivered to either eye to measure eye suppression. Third, the test stimulus was made similar in features (such as shape and contour) to one, but not the other, rivalry-inducing stimulus to demonstrate feature suppression.

If eye suppression is borne out, the implication is that binocular rivalry is initiated in monocular cells of the cortex, and therefore in or before the primary visual cortex. If feature suppression is supported, the initiation must be in an area beyond that in which monocular cells are prevalent. It is important to resolve this controversy because it could help to solve a fundamental question about the perceptual process: is the switch from one percept to another triggered by low-level neural events, or does it require feedback from higher visual cortex?
Predictions of the hypotheses

The stimuli are shown at the bottom of Figure 5.1. A circle presented to one eye and a star-like stimulus to the other were used to induce binocular rivalry. The test stimulus, comprising two distorted semicircles, was designed to be similar in features, including the shape and contour, to the rivalry-inducing circle. The circular rivalry-inducing stimulus was presented to either left or right eye and the test stimulus was presented briefly to the right eye or to both eyes. Figure 5.1 summarises the predictions of the eye suppression and feature suppression hypotheses in the resulting three cases.

Eye suppression is a loss of sensitivity to stimuli delivered to a specific eye. The loss does not depend on the type of stimulus, and there is no sensitivity loss for stimuli delivered to the fellow eye. On the other hand, feature suppression is a loss of sensitivity to stimuli specific to feature. The loss does not depend on the eye to which the stimulus is delivered, and there is no sensitivity loss for stimuli with differing features.

Consider eye suppression first (upper part of Figure 5.1). The left side of its graph shows the case where the rivalry-inducing stimulus comprised a star to the left eye and a circle to the right eye. The test was presented to just the right eye. When the right-eye’s rivalry-inducing stimulus (the circle) is dominant (open symbols) the tested eye is dominant and the hypothesis requires that sensitivity be high. But when the circle is suppressed (filled symbols), the tested eye is suppressed and sensitivity is therefore reduced. By the same logic, the sensitivities for the data points in the middle of the graph are the same as those on the left side of the graph. At the right of the graph, where the stimulus was delivered to both eyes, sensitivity is determined by the dominant eye and is therefore high regardless of which eye is dominant.
The predictions of the feature suppression hypothesis are shown in the lower part of Figure 5.1. The test is circle-like, so that sensitivity is high whenever the dominant stimulus is circular. Conversely, dominance of the star indicates suppression of the circle, and therefore reduced sensitivity.

**Figure 5.1.** Predictions of the eye and feature suppression hypotheses. Vertical axes give visual sensitivity while the horizontal axes give the test conditions. For each test condition, the rivalry-inducing and test stimuli are shown below the horizontal axis. Open symbols represent the sensitivities during dominance phase of the right-eye, while the filled ones represent those of the suppression phase. Under the eye suppression hypothesis, sensitivity is low when the test stimulus is presented to the suppressed eye. Feature suppression hypothesis predicts that sensitivity is low when the test stimulus has similar features to the suppressed stimulus.
Experiment 1: Circular test stimulus

Methods

Stimulus generation, the optical arrangement, and binocular alignment are described in the General Methods chapter. The rivalry-inducing stimuli, illustrated below the horizontal axis of Figure 5.2B, consisted of a circle and a star-like stimulus, both with a peak contrast of 0.45. The star-like stimulus was a radial pattern, calculated in two stages. First, a radial grating was computed: at any given radius, luminance in this grating was a sinusoidal function of the angle between the radius and horizontal axis. The frequency and phase of the sinusoid were set so that the grating had ten cycles, and luminance was maximal along the horizontal diameter. Second, the grating was masked so that it appeared only in an annular region corresponding to the circle. The mask was a Gaussian function of the distance from the centre of the grating. At each point of overlap, the circle and star-like stimulus were mutually perpendicular, evoking robust binocular rivalry.

The circular test stimulus was formed by adjoining a 1.5-lobed and a 2-lobed semicircle along the central horizontal line of the fusion border. Its contrast, 0.45, was equal to that of the rivalry-inducing stimulus. The post-test mask was formed by superposition of two circles which were 3-lobed and 4-lobed, had the same amplitude as the test stimulus, and half its contrast.

Three subjects, AK, DL and MH, with ages ranging from 28 to 36, participated in the experiments. They were familiar with the psychophysical tasks, but apart from the author, DL, were unaware of the experimental purpose. During binocular rivalry, subjects triggered a test stimulus when the rivalry-inducing stimulus to the right-eye was dominant or suppressed. The test was added to the inducing stimulus for 120 ms. From trial to trial, test lobes were randomly rotated.
and the 2-lobed semicircle was at either the top or bottom: subjects were required to indicate where it appeared. The test lobe amplitude was adjusted to provide 80% correct responses.

The experiment had three test conditions. In the first and second conditions, the test stimulus was delivered to the right eye, and its features were similar and dissimilar to the right-eye rivalry-inducing stimulus accordingly. The third condition had the test stimulus delivered to both eye and its feature was similar to the right-eye rivalry-inducing stimulus. The order of the three test conditions was randomised to minimise biases due to tiredness or loss of concentration.

**Results**

The three subjects all reported robust binocular rivalry while viewing the inducing stimulus. The results are shown in Figure 5.2A. The vertical axis shows sensitivity, calculated as the reciprocal of lobe amplitude threshold, and error bars give 95% confidence intervals. Open symbols represent the thresholds measured while the right-eye rivalry-inducing stimulus was dominant, and the filled symbols are for the stimulus suppressed. The mean threshold across all data in part A of the figure was 5.8%. For this threshold, the test stimulus appears similar to the circular rivalry-inducing stimulus, as illustrated in Figure 3.2 of the *General Methods* chapter. This similarity between the test and one of the rivalry-inducing stimuli satisfies one of the requirements of the experimental design. Figure 5.3B shows the normalised sensitivities for comparison across subjects. These relative sensitivities were obtained by dividing the sensitivities for each subject by the mean of the three dominance values for the same subject.
Figure 5.2. A. Visual sensitivity measured with the circular test stimulus. The vertical axes give sensitivity, which is the reciprocal of the threshold test lobe amplitude, while the horizontal axis gives the test conditions. Open symbols represent the sensitivities during the dominance phase of the right eye, while the filled ones represent those of suppression. The three subjects had similar results, which match the prediction of the eye suppression hypothesis. B. Relative sensitivity, obtained by dividing the sensitivity for each subject by the mean of the three dominance values for the same subject.
The hypothetical sensitivities from eye and feature suppression are given algebraically in Table 5.1. The empirical data appear to match the predictions of the eye suppression hypothesis well, and to fit poorly with the feature suppression predictions. This conclusion was checked by fitting a regression equation, 

\[
\text{sensitivity} = b_1 e + b_2 f + b_3 f + e,
\]

to the logarithmic data: \( e \) and \( f \) (as shown in Table 5.1) are the predictions of the eye and feature suppression hypotheses, respectively, \( b_1 \), \( b_2 \), and \( b_3 \) are the least-squares regression coefficients, and \( e \) is residual error. The data used were the logarithms of the normalised sensitivities from all three subjects. The coefficients, along with their 95% confidence intervals, were \( b_1 = -0.394 \pm 0.070 \), \( b_2 = 0.008 \pm 0.066 \), and \( b_3 = 0.003 \pm 0.052 \). The first coefficient indicates that eye suppression produces a sensitivity loss of about 0.4 log units, consistent with previous findings (Blake & Camisa, 1979; Nguyen, Freeman & Alais, 2003; Nguyen et al., 2001). The confidence interval for \( b_1 \) includes zero, consistent with an absence of feature suppression.

<table>
<thead>
<tr>
<th>Dominant inducing stimulus</th>
<th>Inducing stimulus to tested eye</th>
<th>Eye suppression, ( e )</th>
<th>Feature suppression, ( f )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circle</td>
<td>Circle</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Star</td>
<td>-1</td>
<td>0</td>
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<tr>
<td></td>
<td>Both</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Star</td>
<td>Circle</td>
<td>-1</td>
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<td>Both</td>
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</tbody>
</table>

*Table 5.1.* Loss of sensitivity predicted by the eye and feature suppression hypotheses. The sensitivity loss predicted by eye suppression, in logarithmic units, is \( de \), where \( d \) is the suppression depth and \( e \) is tabulated. Similarly, the sensitivity loss due to feature suppression is \( df \).
Experiment 2: Star-like test stimulus

The initial evidence favours the idea of eye suppression. To make sure, however, that the evidence was not biased by the choice of test stimulus, the experiment was repeated with the star as test stimulus for the same three subjects.

Methods

The rivalry-inducing stimulus had the same form as that in Experiment 1 but had a peak contrast of 0.9. The star-like test stimulus (Figure 5.3A) also had a contrast of 0.9. It contained a half-star with more than five arms, and a second half-star with fewer than five; the number of arms totalled ten. The threshold variable was arm imbalance, defined as one tenth of the difference in arm number between the two half-stars. The imbalance ranged from 0 to 1, and Figure 5.3B illustrates a series of test stimuli with differing imbalances.

On each trial, the test stimulus replaced the rivalry-inducing stimulus of one or both eyes for 120 ms. Arm location within each half-star was randomised from trial to trial to eliminate local cues. The test was followed immediately by a mask, which consisted of two superimposed stars. The rationale for the post-test masking has been detailed in Experiment 2 of Chapter 4. One star in the mask had the arm spacing of one of the half-stars in the test, and the other star had the spacing of the other half-star; arm location in the mask was randomised. The subject’s task was to nominate which half of the test stimulus had more arms. The threshold variable, the arm imbalance, was adjusted to obtain 80% correct responses.
Figure 5.3. Star-like test stimuli and their post-test masks.  
A. Test stimulus within a fusion border. The test stimulus was formed from two adjacent semi-stars with differing numbers of arms. From trial to trial, the arms were rotated randomly around each semi-star and the semi-star with more arms was either at the top or bottom.  
B. When the imbalance is small, the top and bottom semi-stars are similar, making the stimulus appear similar to the star-like rivalry-inducing stimulus.  
C. The post-test masks. Each is formed by superimposing two star-like stimuli. Each component has an arm spacing matched to that of either the top or the bottom semi-star.
Results

The three subjects had similar results as shown in Figure 5.4A. The mean threshold imbalance was 7.2% across all data in part A of the figure. Test stimuli with an imbalance close to this value can be seen in Figure 5.3: they appear similar to, and therefore shares features with, the star-like rivalry-inducing stimulus.

Data, normalised by dividing the sensitivities for each subject by the mean of the dominance values for that subject, are shown in Figure 5.4B. The hypothetical sensitivities from eye and feature suppression are given algebraically in Table 5.1. Fitting of the sensitivity equation to the combined data yielded $b_1 = -0.294 \pm 0.057$ and $b_2 = -0.018 \pm 0.054$, and $b_3 = 0.012 \pm 0.042$ (please refer to the result session of Experiment 1). The confidence interval for the feature suppression coefficient $b_2$ includes zero, and the results obtained with the star-like test stimulus therefore correspond with those of the circle-like test: the data match the predictions of the eye suppression hypothesis well, and are a very poor match with the feature suppression predictions.
Figure 5.4. Visual sensitivity measured with the star-like test stimulus. **A.** Sensitivity was calculated as the reciprocal of the threshold arm imbalance measured during the right-eye’s dominance (open symbols) or suppression (filled symbols) phases of rivalry. The vertical axes give sensitivity while the horizontal axis gives the test conditions. The three subjects had similar results, matching well with the predicted results from the eye suppression hypothesis. **B.** Normalised sensitivity, which gives sensitivity divided by the mean of the dominance values in the three test conditions for each subject.
5. Eye & feature suppression

Discusson

Masking effects
There is a slight mismatch between the empirical results and the prediction of the eye suppression hypothesis in that both dominance and suppression sensitivities were lower in the first test condition (the left side of the graphs) than in the second one (the middle of the graphs) of Figure 5.4. This presumably reflects the stimulus masking effect caused by the similarity between the rivalry-inducing stimulus and the test stimulus. The masking in the condition at the left of the graph was monocular, and in the other cases, it was interocular. The magnitude of monocular masking is stronger than that of interocular masking (Breitmeyer, 1984), resulting in lower sensitivity in the first case. This sensitivity difference is absent in Figure 5.2, perhaps because the test stimulus was superimposed on the rivalry-inducing stimulus in this case, rather than replacing it; superposition may have reduced temporal masking. In general, the influence of masking is small, and does not interfere with the comparison of the eye and feature suppression hypotheses.

Discrepancy of eye and feature suppression
The results show that sensitivity is lower for stimuli presented to an eye during its suppression phase than for stimuli presented during dominance, and that sensitivity is lowered for differing forms of the test stimulus. This agrees with the finding that changes in the orientation or spatial frequency of the suppressed stimulus can go undetected during rivalry (Blake & Fox, 1974a; Nguyen et al., 2001). Conversely, while the experiments were designed to reveal the presence of feature suppression, the current results give clear evidence against it. Previous authors have detected the presence of feature suppression: how is this discrepancy resolved? The clearest evidence for feature suppression comes from Logothetis et
al. (1996), who swapped rivalrous stimuli between the eyes three times a second, but found dominance intervals that spanned several swaps. They also flickered their stimuli at a frequency of 18 Hz, and it has been shown subsequently that the flicker is a necessary condition for normal dominance intervals during the swapping experiment (Lee & Blake, 1999). Wilson (2003) modelled this behaviour, and showed that flicker shifted coherent activity from the monocular stage of his model to the binocular stage, making it more like feature rivalry. It seems, therefore, that feature suppression can only be seen if the usual mutual inhibition between monocularly-driven cells is prevented.

There are other studies whose results may appear to favour the feature suppression hypothesis. Watson, Pearson & Clifford (2004) used stimuli representing walking humans visible only through lights attached to their joints. When one walker was presented monocularly and a walker moving in the opposite direction was presented to the other eye, robust rivalry between the walkers ensued. Given the high-level perceptual grouping required to interpret a set of moving lights as a walker, this suggests that feature suppression is at work. However, a control experiment in which walkers were split between the eyes yielded weak rivalry, indicating that eye rivalry was the major effect. Watson et al. interpreted their results as showing that rivalry is exerted at a low level but is biased by top-down feedback favouring an ecologically-plausible percept. The same interpretation presumably applies to the coherent percept obtained during simultaneous colour rivalry at multiple visual field locations (Kovács, Popathomas, Yang & Fehér, 1996). It seems, though, that at least some top-down biases are small relative to bottom-up factors because subjects have very little success when asked to consciously maintain one rivalrous percept at the expense of the other (Meng & Tong, 2004).
5. Eye & feature suppression

Initiation of binocular rivalry

The results can therefore be further interpreted as follows. Eye suppression assumes inhibition between cells driven by the left eye and cells driven by the right. This inhibition could take place in the lateral geniculate nucleus or in the input layer of the primary visual cortex, both of which contain neurons with excitatory drive from only one eye. Neurons in visual cortex higher than the primary area, however, are almost exclusively binocular (Burkhalter & Van Essen, 1986) so that the inhibition between monocularly-driven cells is unlikely to take place there. We are therefore forced to the conclusion that the sensitivity losses recorded in our experiments originate in mutual inhibition between left- and right-eye-driven cells in the lateral geniculate nucleus or the primary visual cortex. Feature suppression, on the other hand, is only revealed by disabling eye suppression or as a top-down bias secondary to the effects of eye suppression.
5. Eye & feature suppression