Brain and Mind **2:** 39–54, 2001.

On the Relationship Between Interocular Suppression in the Primary Visual Cortex and Binocular Rivalry

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(Received: 8 December 2000; accepted: 26 February 2001)

Abstract. Both classical psychophysical work and recent functional imaging studies have suggested a critical role for the primary visual cortex (V1) in resolving the perceptual ambiguities experienced during binocular rivalry. Here we examine, by means of single-cell recordings and optical imaging of intrinsic signals, the spatial characteristics of suppression elicited by rival stimuli in cat V1. We find that the "interocular suppression field" of V1 neurons is centred on the same position in space and is slightly larger (by a factor of 1.3) than the minimum response field, measured through the same eye. Suppression is always strongest at a single position corresponding very closely to the centre of the classical receptive field, and reduces responses through the other eye by up to 90% but typically around 40%. The spatial pattern of interocular suppression, as revealed by optical imaging, closely matches the cortical representation of the stimulus, which is being suppressed, both in terms of its orientation and the eye of origin. These results indicate that interocular suppression is directly related to the functional architecture of V1; it is probably caused by direct inhibitory interactions between neighbouring cortical columns of opposite ocular dominance.

Introduction

In recent years, binocular rivalry has become a popular paradigm for the study of neuronal mechanisms underlying perceptual selection processes and awareness. The latest neuro-physiological investigations tend to support the notion that high-level visual areas are the "seat" of our alternating percepts during viewing of rival figures, or in other words the place where rivalry is fully resolved and neuronal responses correlate with perception (Sheinberg and Logothetis, 1997; Tong *et al.*, 1998). The source of the "gating signal" that triggers the adoption of one or the other percept has been placed in the (right) parietal cortex (Lumer *et al.*, 1998; Miller *et al.*, 2000). However, these findings should not detract from the fact that conflicting inputs representing non-fusible retinal images first need to be integrated in the primary visual cortex, V1. All perceptual interpretations are likely to be based on the output of neurons in this area, which is essential for virtually all

conscious visual experience, regardless of where binocular rivalry is ultimately resolved. Indeed, until recently, most models of binocular rivalry assumed that the phenomenon were based on alternating dominance and suppression of the two eyes' inputs into V1 (Blake, 1989; Lehky and Blake, 1991).

Therefore, it is not surprising that some of the first investigations into the neural substrate of binocular rivalry were concerned with responses of neurons in V1 and in the lateral geniculate nucleus (LGN), which provides exclusively monocular input to V1. While some LGN cells exhibit a reduction of responses to binocular stimuli relative to monocular stimuli presented to the dominant eye, this suppression is not specific for rival stimulus pairs but occurs with fusible pairs as well (Moore *et al.*, 1992) (Sengpiel *et al.*, 1995a). Earlier studies of the primary visual cortex, using dichoptic grating stimuli, found strong binocular interactions, both facilitatory and inhibitory, when the two gratings were of the same or similar orientations. These were interpreted as neural correlates of binocular fusion and depth perception (Blakemore *et al.*, 1972; Ohzawa and Freeman, 1986). However, those studies failed to reveal binocular interactions with rival (orthogonal) gratings, which were first described by Sengpiel and Blakemore (1994). Notably, it is only among binocular V1 neurons that stimulus-specific suppression of binocular responses below the level of monocular responses is observed (Sengpiel *et al.*, 1995a). This interocular suppression is likely to contribute to the perceptual experience of binocular rivalry, sharing with it many characteristics such as orientation independence of the strength of suppression (Blake and Lema, 1978; Sengpiel *et al.*, 1995b), and similar thresholds for interocular orientation difference (Braddick, 1979; Sengpiel *et al.*, 1995a) and spatial frequency difference (Blakemore, 1970; Sengpiel *et al.*, 1995b). However, interocular suppression in V1 does not exhibit the waxing and waning that one would expect of a direct neural correlate of alternations of stimulus dominance and suppression experienced during binocular rivalry (Sengpiel *et al.*, 1995a).

We have previously hypothesized that interocular suppression derives from a network of inhibitory connections between neighbouring ocular dominance columns within V1 (Sengpiel and Blakemore, 1994; Sengpiel *et al.*, 1995a; Sengpiel and Blakemore, 1996). As adjacent ocular dominance columns tend to represent very similar regions of visual space, one would therefore predict that the "suppression field" in one eye should be of similar location and extent as the classical, excitatory receptive field of a neuron in the other eye. Moreover, the spatial pattern of interocular suppression (and of binocular facilitation) should closely follow the cortical pattern of ocular dominance columns. Here, we map interocular suppression fields using single-cell recordings, and we visualize overall cortical patterns of suppression by means of optical imaging of intrinsic signals.

Methods

Experiments were performed on juvenile or adult cats bred in laboratory colonies in Oxford and Munich. All procedures were carried out with the approval of the British Home Office or of German local government authorities.

SINGLE-UNIT MAPPING OF INTEROCULAR SUPPRESSION FIELD

Single-unit recording experiments were performed on twelve adult cats. Details of anaesthesia, surgery and recording techniques have been described elsewhere (Sengpiel *et al.*, 1995a; Sengpiel *et al.*, 1998). Briefly, following initial anaesthesia with ketamine, tracheal cannulation was performed, and the animal was artificially ventilated and anaesthetized with a mixture of nitrous oxide (55–65%) and oxygen (35–45%) plus halothane (2% during surgery, 1–1.5% during recording). Respiration rate and volume were adjusted to maintain end-tidal CO_2 at 4.0–4.5%. During recording the animal was paralysed with a continuous i.v. infusion of gallamine triethiodide (10 mg/kg/h) in glucose-saline. E.E.G. and E.C.G. were constantly recorded to monitor the state of anaesthesia. Body temperature was kept at 38 °C. The pupils were dilated with atropine hydrochloride, and the lids and nictitating membranes retracted with phenylephrine. Gas-permeable contact lenses were fitted and 3-mm artificial pupils were placed in front of the eyes, as well as additional lenses to correct focus for the appropriate viewing distance.

The cat viewed, *via* front-silvered mirrors, a pair of high-resolution oscilloscope screens (Tektronix 608; display size, 11 × 10 cm, viewing distance, 57 cm), on which stimuli were presented independently to the two eyes. Drifting, sinusoidally modulated gratings (mean luminance, 21 cd/m^2 and 42 cd/m^2 for binocular and monocular stimulation, respectively) were generated by a 'Picasso' (Innisfree, Huntingdon, UK) image synthesizer. External stimulus control, data acquisition and analysis were performed by a Visual Stimulation software package ('VS'; Cambridge Electronic Design, Cambridge, UK). Optic disc and *area centralis* in each eye were back-projected onto the oscilloscope screens by means of a reversible ophthalmoscope.

Receptive fields of isolated single neurons were first plotted by hand. Receptive fields in the two eyes were carefully centred on the two oscilloscope screens. Full-field gratings were then used to determine preferred orientation and spatial frequency through each eye. Optimal stimuli were presented binocularly to assess phase-selective binocular interactions. The minimum response field was mapped in one eye or sometimes in both eyes by presenting circular grating patches of optimal orientation and spatial frequency (diameter, 1.5 to 3.0 deg) at positions that were randomly varied over a 5-by-5 evenly spaced grid. The spacing and overall size of the grid were chosen according to the hand-mapped receptive-field size. The maximal spacing and area were 4 deg and 8 by 8 deg, respectively. Finally, binocular interaction fields were mapped by continuously stimulating one eye (usually the dominant eye) with an optimal full-field grating ("conditioning

stimulus") and presenting to the other eye circular grating patches ("probe stimuli") at the same 25 positions that had been used to map the minimum response field. (If the minimum response field had been mapped only in the other eye, retinally corresponding positions were chosen.) For these probe stimuli, gratings of optimal or orthogonal-to-optimum orientation were used. Stimuli were displayed for 1.5–2.0 s, interleaved with periods lasting 1.5 s during which the conditioning stimulus alone was displayed. Average response rates for a minimum of 5 complete trials were obtained for each of the 25 probe stimulus positions and percentage changes of response with respect to the average response to the conditioning stimulus were computed as *Response change* (x,y) = $(R_{\text{probe}}/R_{\text{conditioning}} - 1) \cdot 100\%$.

OPTICAL IMAGING OF SPATIAL PATTERN OF INTEROCULAR SUPPRESSION

Optical imaging experiments were performed on nine cats ranging in age from 10 weeks to 1 year. The anaesthetised and paralysed animals (details, see above) viewed, via front-silvered mirrors, a large tangent screen at 1 m distance onto which stimuli were projected that were controlled independently for the two eyes (STIM, Rockefeller Institute, New York City, NY). Images of the intrinsic signals produced by neuronal activity in response to the different visual stimuli were captured using a cooled slow-scan CCD camera or an enhanced differential imaging system (ORA 2001 or Imager 2001, Optical Imaging, Germantown, NY), focussed ca. 500 μm below the cortical surface. Optical imaging of intrinsic signals is based on differences in reflectance of incoming red light between active and less active regions of cortex. These are the result of the utilisation of oxygen provided by haemoglobin (deoxyhaemoglobin absorbs light of $>$600 nm more strongly than oxyhaemoglobin) as well as of changes in the light scattering properties of spiking neurons (Bonhoeffer and Grinvald, 1996).

We first obtained maps of orientation preference and of ocular dominance in area 17 according to standard procedures (e.g. Bonhoeffer and Grinvald, 1996), using monocular or matched binocular moving square-wave grating stimuli (0.5 cyc/deg, moving at 2 Hz) of 4 different orientations, interleaved with blank-screen presentations. We then imaged responses to rival stimuli presented either simultaneously or in a staggered fashion (see Sengpiel and Blakemore, 1994). For the latter, gratings were first shown to one eye (usually the ipsilateral), and after a delay of 1.8 s, orthogonally oriented gratings were introduced in the other eye. Six frames of 600 ms duration were collected during each 3.6 s rival stimulus presentation, followed by a 9 s inter-stimulus interval, which allowed for metabolic relaxation. Images were high-pass filtered and signal amplitude was displayed on an 8-bit grey-scale (for details of analysis, see Results).

Results

Here we first describe, for individual neurons, the spatial characteristics of the field in one eye, where grating stimuli produce suppression of responses to an orthogonal grating in the other eye. We then visualize the spatial extent of suppression caused by orthogonal grating pairs, or in other words, the populations of neurons, whose firing is suppressed by rival stimuli.

SPATIAL MAPPING OF INTEROCULAR SUPPRESSION FIELD

We recorded a total of 70 neurons, although not all of the binocular interaction protocols could be completed for all cells. For each cell, we calculated the size of the minimum response field (MRF) from the two-dimensional plot of responses to the optimal probe stimulus presented monocularly in a 5-by-5 grid of positions. Response rates between discrete positions were interpolated linearly, and the MRF was defined as the cross-sectional area for which the response equalled half of the maximal response, reduced by the spontaneous activity (see Sun and Bonds, 1994). Due to the limited resolution of sampling, this method yielded a relatively coarse estimate of MRF area; nevertheless it agreed well with the receptive-field hand-plots and provided a point of reference for the binocular interaction fields. Binocular interaction fields were quantified in a similar fashion, with the half-maximal level defined as the mid-point between the maximal change in response (either positive or negative), relative to the conditioning stimulus response, and zero change.

The most immediately obvious finding of our study was the close spatial match between the excitatory and suppressive binocular interaction fields and the minimum response field in the eye under consideration. This is exemplified in Figure 1 for a complex cell recorded from the infragranular layers. The area of the minimum response field in the non-dominant eye was calculated to be 11.8 deg^2 (Figure 1A). The binocular facilitation field in that eye, tested with optimally-oriented grating patches against a conditioning full-field stimulus of optimal orientation in the dominant eye, was considerably smaller (3.0 deg^2) but centered on the same location in the visual field (Figure 1B). More importantly, the interocular suppression field, tested with orthogonal-to-optimum grating patches in the non-dominant eye against a conditioning full-field stimulus of optimal orientation in the dominant eye, was found at the same position as the minimum response field and covered roughly the same area in visual space (Figure 1C). In fact, at 17.3 deg^2 it was marginally larger.

Another example of facilitatory and suppressive binocular interaction fields is shown in Figure 2 for a supragranular simple cell. In this case, the suppression field (2.8 deg^2) was again larger than the facilitatory field (1.8 deg^2), but only moderately so. In our sample of cells, the interocular suppression field was consistently slightly larger than the minimum response field assessed with grating patches, the average ratio being 1.3 (geometric mean). In contrast, the suppression field was generally

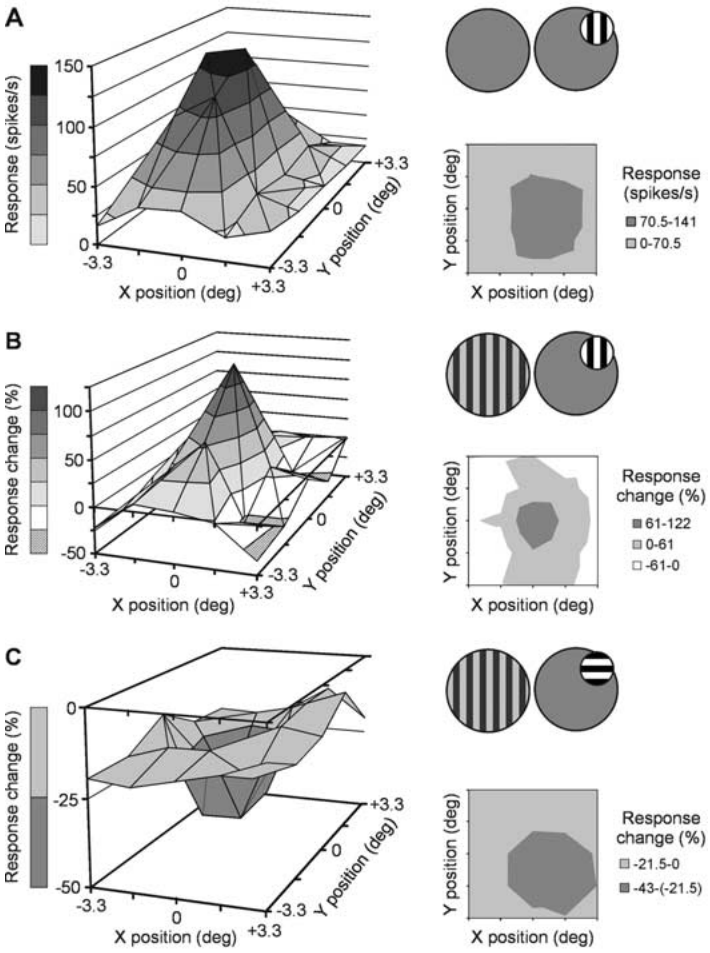

Figure 1. Monocular minimum response field profile (A) and binocular interaction fields (B, C) in the non-dominant (ipsilateral) eye of a complex cell recorded from infragranular layers. The binocular facilitation field (B) was determined with an iso-oriented and the interocular suppression field (C) with an orthogonally oriented probe stimulus. The two-dimensional response profiles shown correspond to a square region of the visual field extending over 6.6 by 6.6 deg centred on the cell's receptive field. For all three profiles the probe patch stimulus was 3 deg in diameter (contrast, 80%), centred on sample positions separated by 1.65 deg. The conditioning full-field stimulus displayed to the dominant eye in (B) and (C) had a contrast of 20%. x and y position refer to the position of the probe stimulus relative to the centre of the cell's receptive field. The x dimension runs orthogonal and the y dimension parallel to the cell's preferred orientation. The experimental conditions are represented pictorially in each sub-figure. Responses and response changes, respectively, represent the average of 10 trials (A) or 8 trials (B, C). The lowest average response (greatest suppression) recorded in response to the orthogonal probe patch (C) is found at the same sample position as the largest response rate obtained with the optimally oriented patch probe, either alone (A) or in combination with stimulation of the other eye (B). Insets below stimulus pictograms show top-down views of thresholded response profiles. The darkest (central) area corresponds to the region exceeding the half-maximal response (A) or response change (B, C).

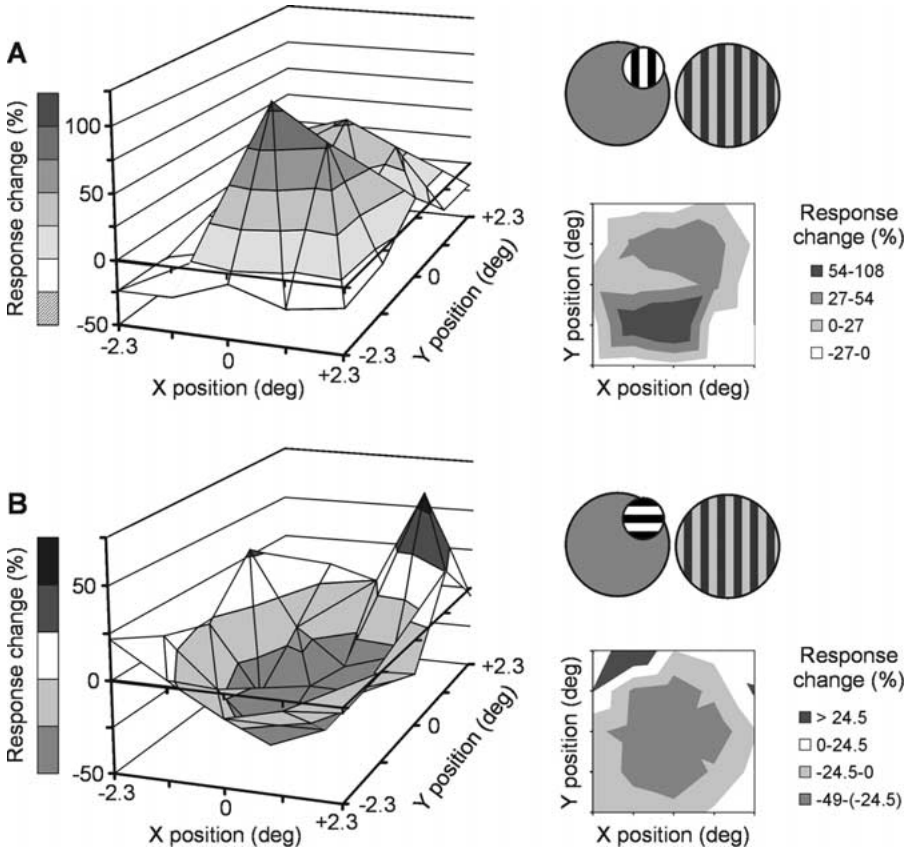

Figure 2. Binocular interaction fields in the left (ipsilateral) eye of a simple cell recorded from supragranular layers. The binocular facilitation field (A) was determined with an iso-oriented and the interocular suppression field (B) with an orthogonally oriented probe stimulus. For both response profiles the probe patch stimulus was 2 deg in diameter (contrast, 80%), centred on sample positions separated by 1.15 deg. The conditioning full-field stimulus displayed to the right (contralateral) eye had a contrast of 20%. Data shown represent the average of 15 trials. For the inset in (A), the darkest area corresponds to the region of half-maximal facilitation. For the inset in (B), the medium-grey (central) area corresponds to the region of half-maximal suppression. Note that each probe stimulus produces interactions of the opposite sign when presented in more peripheral locations compared with central locations.

much larger than the binocular facilitation field, the geometric mean ratio being 3.1.

For all neurons, interocular suppression was strongest at a single central position that corresponded as closely to the centre of the classical receptive field in the same eye as could be ascertained within the resolution limits of our stimulus protocol. In the most extreme cases, responses to the conditioning stimulus were suppressed by as much as 90% (see Figure 3), while peak suppression of around 40% was common. Outside the zone of suppression, we occasionally observed a

facilitatory effect of orthogonal-to-optimum grating patches, such as illustrated in Figure 3A. This effect is similar to the surround facilitation that has been described for monocular stimulation in cat and monkey V1 (Sillito *et al.*, 1995). However, this was a transient phenomenon, occurring within the first second of onset of the orthogonal probe stimulus. In contrast, interocular suppression always built up within the first second after stimulus onset and then persisted at a stable level (Figure 3B).

OPTICAL IMAGING OF SPATIAL PATTERNS OF INTEROCULAR SUPPRESSION

The close correlation between the interocular suppression field and the classical receptive field suggests a substrate for interocular suppression within the local horizontal circuitry of V1. We therefore imaged population responses to rival gratings with a stimulus paradigm very similar to that used for single-unit recordings.

In all animals tested, rival stimuli simultaneously presented to both eyes revealed only weak binocular interactions. We compared responses to rival gratings with monocular responses to each of the two gratings making up the rival pair. The differences between a binocular (rivalry) response and a monocular response through the ipsilateral eye (Figure 4C) were generally greater than the differences between a binocular response and a monocular response through the contralateral eye (Figure 4D). We found that the additional, rival grating primarily caused excitation in cortical domains of the corresponding orientation preference, as evidenced by dark regions of increased absorption (i.e. heightened activity). It also appeared to cause depression of activity in intervening regions, which exhibited slight decreases in absorption. However, in the absence of a direct control, the significance of this effect was difficult to judge.

We therefore developed a paradigm that included such a control and also yielded stronger suppression. We first mapped out the retinotopy of the imaged region of visual cortex using grating stimuli restricted to the upper (or lower) visual field. We then adjusted the lower (or upper) border of these stimuli (close to the horizontal meridian) such that it was represented on the imaged region of cortex (Figure 5). In order to image responses during binocular rivalry, we showed full-field gratings to one eye (usually the eye ipsilateral to the imaged cortical hemisphere), and after a delay of 2 s, orthogonally oriented gratings were introduced in the other eye, on one side of the previously determined border. This paradigm offers the advantage that binocular interactions can be assessed directly by comparing responses in the portion of cortex exposed to rival stimulation to those in the region that received monocular input only.

As expected, the onset of rival stimulation in one half of the visual field did not cause a response in the region of cortex where the other half was represented. Division of rivalry and pre-rivalry responses in that region of cortex therefore yielded a uniform grey. In contrast, in the part of cortex where the rival stimulus was represented, its onset produced excitation in domains preferring its particular orientation

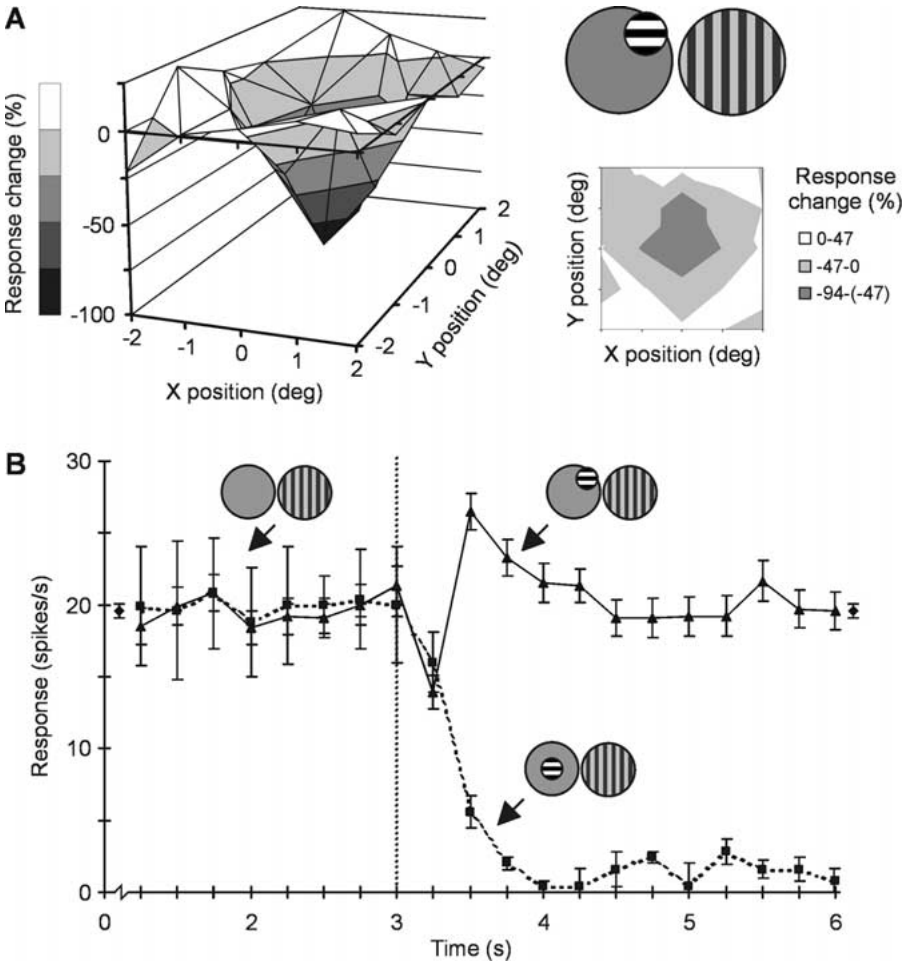

Figure 3. (A) Binocular interaction field in the left (ipsilateral) eye of a simple cell, determined with an orthogonally-to-optimum oriented probe stimulus. The probe patch was 1.5 deg in diameter (contrast, 80%), centred on sample positions separated by 1 deg. The conditioning full-field stimulus displayed to the right (contralateral) eye had a contrast of 20%. Data shown represent the average of 10 trials. (B) Time-course of interactions mediated by the orthogonal probe stimulus placed either in the centre of or outside the cell's minimum response field. Each trial lasted 6 s, and the orthogonal probe was introduced at 3 s (as indicated by the dotted vertical line) in each trial. Prior to this, the cell received an optimal monocular conditioning stimulus (see schematic representations of the stimuli). The dashed line and square symbols show the average response recorded when the orthogonal probe stimulus was placed in the centre of the position matrix; suppression in this case exceeds 90% of the conditioning response level. The solid line and triangles give the average response rate recorded at two peripheral positions. There was a transient facilitatory effect, which was strongest during the first several hundred milliseconds. The diamonds at the left and right of the graph indicate the average response during the monocular conditioning phase.

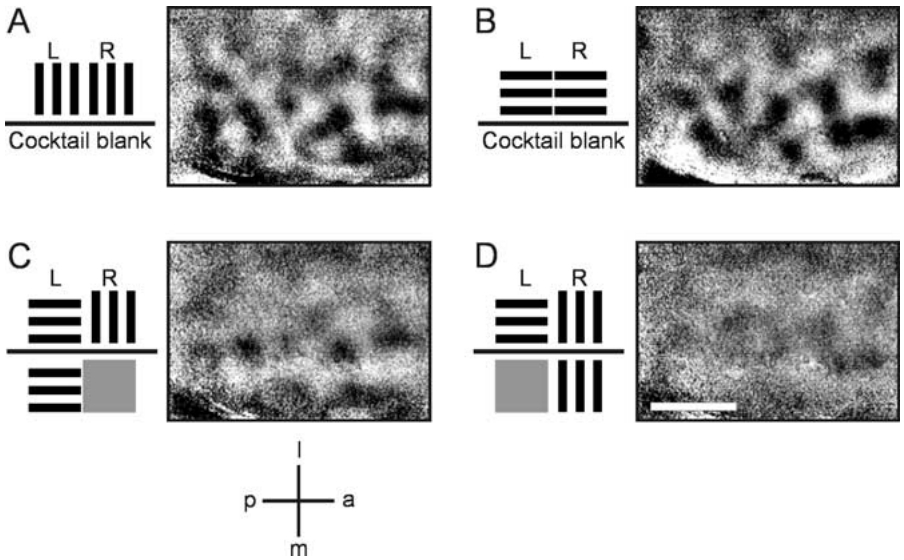

Figure 4. Optical imaging of interocular suppression elicited by simultaneous onset of rival gratings. Activity maps from the primary visual cortex of the left hemisphere (imaged area, 3.0 by 2.2 mm) are shown; scale bar, 1 mm. Note that dark regions correspond to increased, light regions to decreased activity. (A) Response to vertical gratings presented binocularly. The actual response is divided by the "cocktail blank", which represents the sum of responses to gratings of 0°, 45°, 90° and 135° (Bonhoeffer and Grinvald, 1996). (B) Response to horizontal gratings presented binocularly. (C) Response to rival (horizontal and vertical) gratings as compared with the response to a horizontal grating in the left (ipsilateral) eye alone. (D) Response to rival (horizontal and vertical) gratings as compared with the response to a vertical grating in the right (contralateral) eye alone. Binocular stimulation with rival gratings, as compared with monocular stimulation of the ipsilateral eye (C), results in both local facilitation and weak suppression. When comparing binocular stimulation and monocular stimulation of the contralateral eye (D), the interactions are much weaker.

(Figure 6B, C), the overall pattern of which closely matched the standard orientation map (see Figure 6A). Invariably, it also caused clear suppression in regions previously responding to the first stimulus. The close match between areas of suppression and domains responding best to the orientation of the first stimulus was emphasized by 2-dimensional cross-correlation analysis. For the animal illustrated in Figure 6, r values of -0.52 and -0.60 were obtained for the horizontal (Figure 6C) and the vertical rival grating (Figure 6D), respectively. The fact that shifting one map relative to the other always resulted in correlation coefficients closer to zero shows that this correlation was not spurious.

The pattern of suppression illustrated in Figure 6B, D is specific for the combination of grating orientations chosen. In order to obtain a pattern that reflects eye-specific suppression independent of stimulus attributes such as orientation, we added up interaction maps for all combinations of orientations tested. The result is shown in Figure 6E; from a comparison with the ocular dominance map

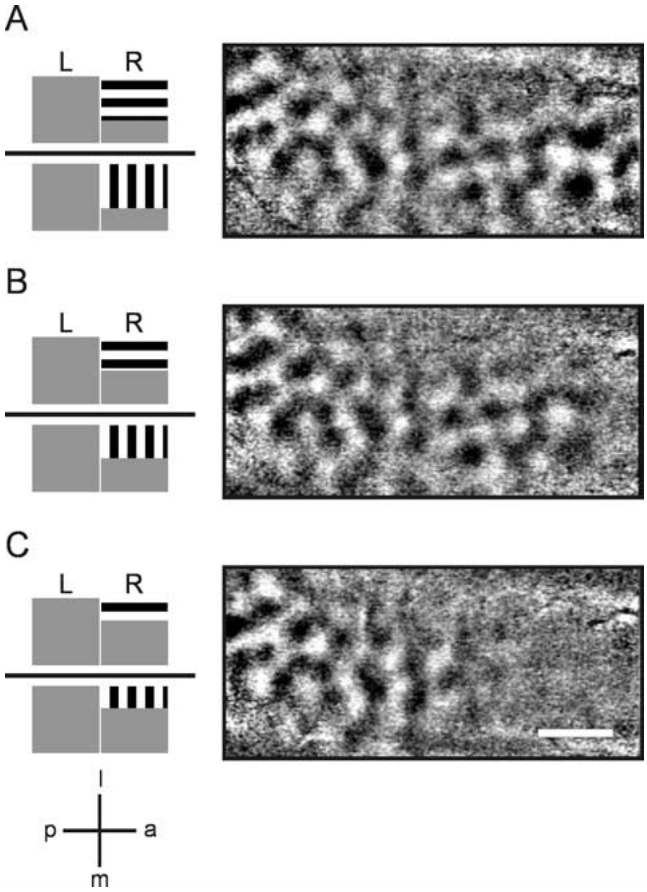

Figure 5. Optical imaging of responses in V1 to gratings restricted to the upper visual field in the right eye. The border of the stimulated region shifts towards the posterior pole (left) as the stimulus border moves upwards (by 2 deg, when comparing A *vs.* B and B *vs.* C respectively), as expected on the basis of the retinotopic space map of cat area 17. Images were obtained from an area of 5.7 by 2.6 mm of the left hemisphere; scale bar, 1 mm.

(Figure 6F) it is apparent that zones that exhibit strongest rivalry-related suppression coincide with domains dominated by the eye that was stimulated first (the left eye in this case). Two-dimensional cross-correlation analysis yielded $r = -0.64$. For another animal, for which records with the same set of rival stimulus pairs could be completed, we obtained $r = -0.62$. These results indicate that interocular suppression in V1 is directly related to the ocular dominance functional architecture.

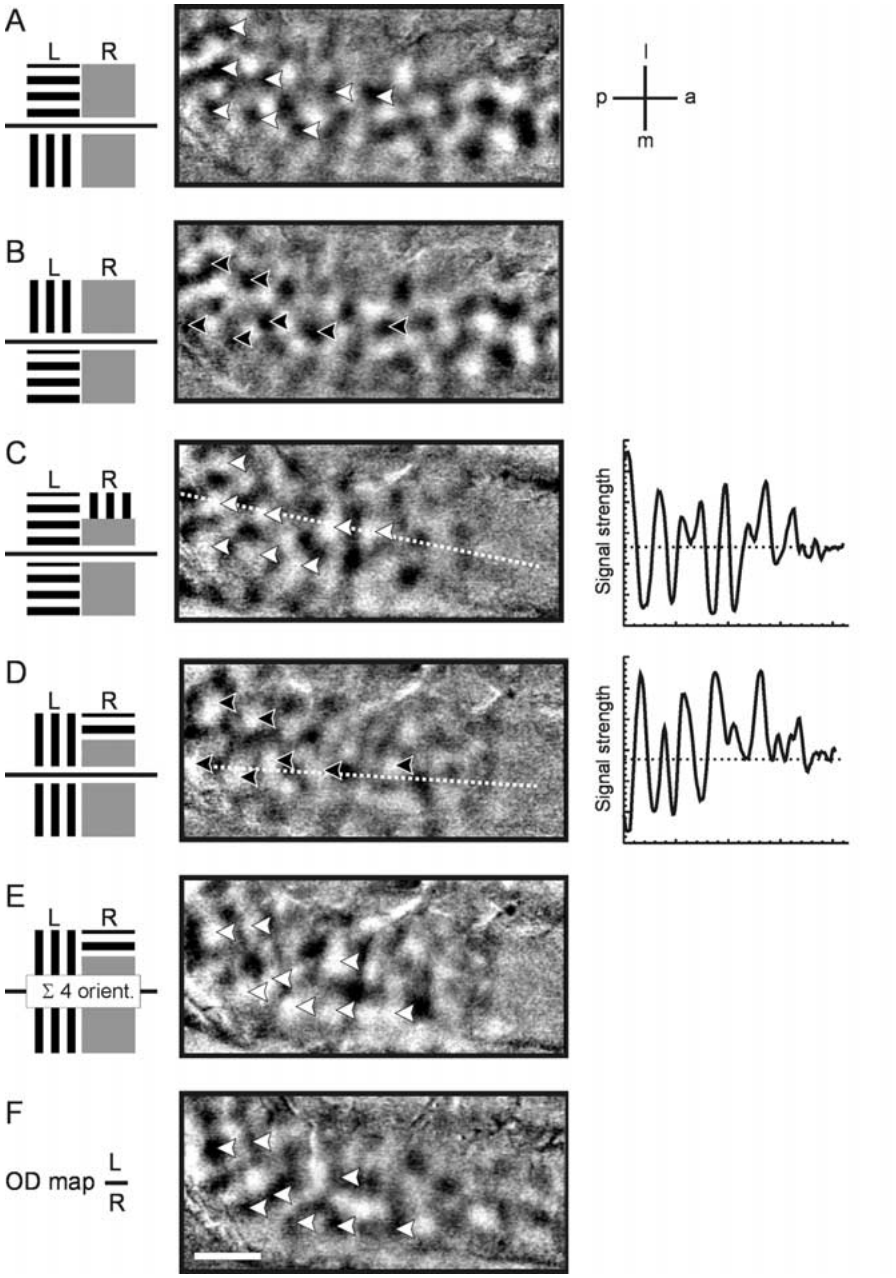

Figure 6. Optical imaging of interocular suppression elicited by staggered presentation of rival gratings. Activity maps from the same area of V1 of the left hemisphere as in Figure 5 are shown; scale bar, 1 mm. Note that dark regions correspond to increased, light regions to decreased activity. (A) Response to horizontal vs. vertical gratings presented to the left (ipsilateral) eye. (B) Response to vertical vs. horizontal gratings presented to the left eye. (C) Response to a stimulus that is rival in the upper visual field vs. monocular stimulation with

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Discussion

Our study demonstrates that interocular suppression in the primary visual cortex contributes to binocular integration on a fine spatial scale. It is elicited if and only if contours of different orientations (or otherwise different features) are present at exactly corresponding positions on the two retinae. Given the increasing tendency towards positional invariance for neurons at higher stages of visual processing, at least some of the machinery required to detect a situation of binocular rivalry (which occurs when rival stimuli fall on corresponding regions of the two retinae) should reside in V1. The kind of interocular suppression that we have described here and in our earlier work (Sengpiel *et al.*, 1995a; Sengpiel *et al.*, 1995b) seems ideally suited for this purpose. A direct inhibitory interaction between neighbouring cortical columns of opposite ocular dominance appears to be the most likely substrate.

Our regime of introducing rival probe stimuli against a background of response to a monocular conditioning stimulus closely resembles the psychophysical "flash suppression" paradigm (Wolfe, 1984). Under such circumstances, humans invariably perceive the newly presented stimulus, while the conditioning stimulus is suppressed for some time before rival alternations set in. As we collected our data from anaesthetized animals, we preferred this paradigm to one of simultaneous stimulus onset, since it gave us the opportunity to study physiological substrates and spatial characteristics of the suppression experienced during binocular rivalry without having to test the animals' perception explicitly. However, this procedure has the disadvantage of not allowing us to examine the temporal properties of rivalry-related processes in the visual cortex.

The similarities between suppression caused by rival binocular stimuli and suppression by conflicting stimuli presented monocularly are striking. Interocular suppression and suppression caused by superimposed gratings in one eye are both

a horizontal grating in the left eye alone. The rival vertical grating is introduced in the right eye with a delay of 1.8 s compared with the left-eye stimulus and has the same spatial extent as the stimulus that yielded the responses shown in Figure 5C. White arrowheads point at regions of suppression, which correspond well with domains responding best to a horizontal grating (A). The grey level in the more anterior portion of cortex (to the right) that was not stimulated by the upper-field right-eye stimulus provides a direct internal control. Suppression is further illustrated by the profile of response strength (right) along the dotted line drawn on the activity map. (D) Response to a stimulus that is rival in the upper visual field vs. monocular stimulation with a horizontal grating in the left eye alone. The rival horizontal grating is introduced in the right eye with a delay of 1.8 s and has the same spatial extent as the stimulus that yielded the responses shown in Figure 5C. Black arrowheads point at regions of suppression, which correspond well with domains responding best to a vertical grating (B). A profile of signal strength along the dotted line drawn on the activity map is shown on the right. (E) Map of binocular interaction obtained by summing up responses to rival gratings across the four orientations tested (0° and 90°, as shown in parts C and D, plus 45° and 135°) and comparing them to the sum of responses to monocular (left-eye) stimuli of the same orientations. (F) Ocular dominance map comparing left-eye vs. right-eye responses to gratings of the same four orientations. White arrowheads indicate that regions of interocular suppression (E) closely correlate with left-eye ocular dominance columns (F).

essentially non-selective for orientation and broadly tuned for spatial frequency (Sengpiel *et al.*, 1995b; Bonds, 1989; DeAngelis *et al.*, 1992). They also show a very similar spatial response profile, the suppression field being more or less co-extensive with the classical receptive field or minimum response field (this study and Freeman, Sengpiel and Blakemore, unpublished observations; DeAngelis *et al.*, 1992). Monocular suppression is usually interpreted in the context of masking, but it could conceivably serve to disambiguate a visual stimulus that allows two equally plausible interpretations, just as is the case in a situation of binocular rivalry. The most obvious example in support of this notion is that of monocular rivalry elicited by two orthogonal gratings of different colours (Campbell *et al.*, 1973): of two apparently mutually exclusive interpretations, one is perceptually suppressed.

A very recent investigation into physiological correlates of binocular rivalry in humans employed the very same stimulus pair of orthogonal red and green gratings (Polonsky *et al.*, 2000). Using functional magnetic resonance imaging (fMRI), they found that fluctuations in V1 activity accompanying perceptual alternations in rivalry amounted to 55% of activity changes during physical stimulus alternations. These data suggest that, at least in part, disambiguation takes place in the primary visual cortex. An "early" site for rivalry between grating stimuli is also supported by the fact that the angular subtense for whole-stimulus rather than patchwork rivalry is scaled with the retinal eccentricity of the stimuli (Blake *et al.*, 1992). This observation suggests that binocular rivalry is based on interactions between cortical modules that represent discrete spatial zones and that can assume only one of two states (but not a "mixed dominance" state). In humans, the eccentricity-related increase in size of these zones of exclusive visibility follows the V1 magnification factor (Blake *et al.*, 1992). For a "later" site of rivalry in areas where responses are more or less invariant to stimulus size and location, this psychophysical finding might not have been expected. It does, however, agree with our observation that the spatial extent of interocular suppression in V1 is closely correlated with receptive-field size, which in turn is a function of retinal eccentricity (Hubel and Wiesel, 1974).

What is the substrate of interocular suppression in V1? The present results support our earlier hypothesis that it derives from a network of inhibitory connections between neighbouring ocular dominance (OD) columns (Sengpiel and Blakemore, 1994; Sengpiel and Blakemore, 1996). As adjacent OD columns tend to represent very similar regions of visual space, it is to be expected that the "suppression field" and the classical receptive field occupy the same locations and are of similar size. Lateral inhibitory connections within V1 are fairly non-selective for the orientation preference of the neurons involved (Kisvárday *et al.*, 1997); the apparent limitation of binocular rivalry to stimulus pairs with large interocular orientation differences is probably a consequence of the selectivity of binocular facilitation for matching orientations (Sengpiel *et al.*, 1995b). However, the link between interocular suppression and the OD columnar architecture of V1 should

not be misinterpreted to imply that it is monocular (left- and right-eye) neurons that interact. As we and others have shown, rivalry-related suppression is much more likely to involve binocular rather than monocular cells in V1 (Sengpiel *et al.*, 1995a; Leopold and Logothetis, 1996). In cat visual cortex, these binocular neurons represent a clear majority of cells anyway, despite a degree of segregation into OD columns.

In summary, we believe that there is good evidence that for simple stimuli short-range inhibitory interactions in V1 mediate local image disambiguation, thereby contributing to the resolution of binocular rivalry.

Acknowledgements

We thank Imke Gödecke for participation in some of the imaging experiments and Frank Brinkmann for technical assistance. This work was supported by the Medical Research Council, the Oxford McDonnell-Pew Centre for Cognitive Neuroscience and the Max-Planck-Gesellschaft.

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