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Grouping visual features during binocular rivalry

David Alais [1], Randolph Blake *

Vanderbilt Vision Research Center, Department of Psychology, Vanderbilt University, Nashville, TN 37240, USA

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Abstract

During binocular rivalry, portions of one eye's view may be perceptually dominant while other portions are suppressed; at any given moment, overall dominance often resembles a patchwork mixture of the two eyes' views. This study investigates the potency of two Gestalt grouping cues — good continuation and common fate — to promote synchronous fluctuations in dominance of two, spatially separated rival targets. Two grating patches were presented to the left eye paired dichoptically with random-dot patches presented to corresponding right eye locations. The orientations of the two gratings were either collinear, parallel or orthogonal. Gratings underwent contrast modulations that were either correlated (identical contrast changes) or uncorrelated (independent contrast changes). Over 60 s trials, observers pressed one key when the left grating predominated, another when the right grating predominated and both keys when both were concurrently visible. Correlated contrast modulation promoted joint grating predominance relative to the uncorrelated conditions, an effect strongest for collinear gratings. Joint predominance depended strongly on the angular separation between gratings and the temporal phase-lag in contrast modulations. These findings may reflect neural interactions subserved by lateral connections between cortical hypercolumns. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Binocular rivalry; Contrast modulation; Lateral connections; Gestalt grouping; Common fate; Good continuation

1. Introduction

Looking about our visual environment we typically experience no difficulty recognizing the many objects scattered throughout the visual field, including some which are partially occluded. However, the speed and ease of visual recognition belie its complexity. Scene segmentation and object recognition, in fact, are the culmination of neural computations distributed among constellations of neurons at successive stages of processing (Van Essen, Anderson & Felleman, 1992; Logothetis, 1998). Complete object descriptions are thus contained within distributed patterns of activity among arrays of feature-sensitive neurons. How are these distributed representations neurally grouped to signal visually coherent objects? This question, of course, constitutes the classic problem of perceptual organization that was effectively highlighted early this century by the Gestalt psychologists (Wertheimer, 1923). In this paper, we utilize binocular rivalry to examine several stimulus determinants of visual grouping, with an eye toward learning about possible underlying neural mechanisms. We start with a brief description of the spatial characteristics of rivalry that make it particularly well-suited for this purpose.

Dissimilar patterns presented to corresponding areas of the two eyes undergo alternating periods of dominance and suppression (Breese, 1899), with the successive, individual periods of visibility being unpredictable in duration (Fox & Herrmann, 1967). Rivalry rarely involves complete dominance of one entire monocular view, unless the images inducing rivalry are very small in angular subtense (Meenes, 1930). Large rival images usually yield piecemeal dominance, whereby different parts of the two eyes' patterns appear intermixed to produce a dynamic, patchwork appearance. Piecemeal rivalry implies that dominance is established within local 'zones' throughout the visual field. Because of the way dominance scales with retinal eccentricity, it has

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* Corresponding author. Tel.: + 1-615-343-7010; fax: + 1-615-343-5027.

E-mail addresses: alaisd@cdf-lppa.in2p3.fr (D. Alais), randolph.blake@vanderbilt.edu (R. Blake)

[1] Present address: LPPA/CNRS, College de France, 11 place Marcelin Berthelot, 75005 Paris, France.

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been suggested that these zones may correspond to hypercolumns in visual cortex (Blake, O'Shea & Mueller, 1992). On the other hand, dominance phases among neighboring rival targets tend to covary when those targets share common feature attributes such as color (Kovacs, Papathomas, Yang & Fehér, 1997) or motion (Alais & Blake, 1998). This spatial cooperativity suggests that local zones of rivalry interact to promote grouping and, therefore, global dominance during rivalry. What are the stimulus determinants of global dominance and how might they be embodied physiologically?

In this paper, we report the effectiveness of two classic Gestalt grouping cues — good continuation and common fate — in the promotion of global dominance in rivalry. For our work, good continuation and common fate were defined, respectively, by contour collinearity and temporal contrast modulation, both of which can plausibly be related to underlying neural mechanisms.

2. Experiment 1: collinearity promotes global predominance

Good continuation refers to the tendency of spatially distributed features to coalesce into a single, extended object when those features imply a smooth, continuous path (Wertheimer, 1923). An excellent contemporary example of this grouping principle at work is provided by the 'pathfinder' displays consisting of an array of small grating patches. Neighboring gratings whose contours are approximately collinear more readily group to form smooth curves than do grating patches consisting of contours that deviate markedly from collinearity (Field, Hayes & Hess, 1993; Kovacs & Julesz, 1993; Hess & Dakin, 1997). Collinear cooperativity has also been shown in boundary completion with subjective contours (Dresp & Bonnet, 1991).

What underlies good continuation among spatially distributed contours such as 'pathfinder' displays? It is generally believed that lateral connections among cortical neurons play a crucial role in signaling the presence of extended object contours that activate neurons across multiple hypercolumns (Gilbert & Wiesel 1979, 1989; Blasdel, Lund & Fitzpatrick, 1985; Gilbert, 1992; Lund, Yoshioka & Levitt, 1993). Significantly, these lateral interconnections are strongest among cells with similar stimulus preferences, including preferred orientation (Ts'o, Gilbert & Wiesel, 1986; Ts'o & Gilbert, 1988; Gilbert & Wiesel, 1989; Malach, Amir, Harel & Grinvald, 1993). Thus, neurons preferring collinear orientations are more strongly connected than neurons preferring parallel orientations, with interactions between orthogonally tuned cells being weaker still (Nelson & Frost, 1985; Schmidt, Goebel, Löwel & Singer, 1997).

In view of the potency of collinearity to facilitate cooperative cortical responses, we were motivated to ask whether two nearby rival targets would achieve mutual dominance more readily when their contours were collinear as compared to parallel or orthogonal.

2.1. Methods

2.1.1. Observers

One of the authors (DA) and three naïve individuals volunteered as participants. All were experienced psychophysical observers with normal or corrected acuity and good stereopsis. All aspects of this study were approved by the Vanderbilt Institutional Review Board.

2.1.2. Apparatus and stimuli

Stimuli were programmed on an Apple 7600 PowerPC computer using Matlab software and the Psychophysics Toolbox (Brainard, 1997). Displays were presented on a NEC XE21 monitor (1024H × 768V resolution; P104 phosphor; 75 Hz frame-rate) with a mean luminance of 23.67 cd/m^2 and output nonlinearities corrected using calibrated look-up tables. Stimuli were presented separately to the eyes using a mirror stereoscope, with a viewing distance of 107 cm in a dimly lit room. Rival stimuli are illustrated schematically in Fig. 1A. The left eye viewed two, horizontally aligned circular apertures 1.5° in diameter containing 3.33 c/deg sinusoidal gratings at 24% Michelson contrast. Center-to-center separation was 2.0° (0.5° separation of inner edges). The gratings had either the same orientation (both vertical or both horizontal) or different orientations (vertical and horizontal). Apertures in corresponding right-eye locations contained static random dot patterns composed of small, random gray-level squares (5 arcmin). Elsewhere, the video monitor was set to average luminance. New 'noise' patterns were calculated each trial. To steady gaze and aid stable binocular fusion, small black crosses placed centrally between the apertures served as fixation points.

2.1.3. Procedure

Grating orientations over trials were either 'collinear', 'parallel' or 'orthogonal' with their orders completely randomized. Keypresses initiated trials and recorded responses. The left- and right-eye stimuli engaged in vigorous binocular rivalry and observers tracked the periods of dominance of the two grating over 60 s trials. One key was pressed continuously while the left-hand grating was predominant over its partner rival target, and another while the right-hand grating was predominant over its rival target. The small angular subtense of the targets favored complete rivalry: targets appeared and disappeared in their entirety with few instances of mixed dominance.

Raw data comprised the durations of individual periods of dominance and suppression for each grating. A dependent variable termed 'joint predominance index' was calculated as follows. First, all durations in which any grating was visible (i.e. left only, right only, and both simultaneously) were summed. The joint predominance index is the proportion of this total in which both gratings were simultaneously visible. Observers completed each condition eight times, with the joint predominance indices averaged into a single estimate. There were pauses of at least 40 s between trials when the screen was blank except for fixation points. Prior to the experiment, observers completed practice trials to become familiar with the dual tracking task.

2.2. Results and discussion

Results for all four observers were qualitatively similar, so group-averaged data are shown in Fig. 1B. A single factor analysis of variance (ANOVA) revealed a significant effect of grating orientation ($F_{2,6} = 14.99$; $P < 0.005$). The means for collinear and parallel conditions differed significantly ($F_{1,6} = 14.43$; $P < 0.01$), with greater joint predominance in the collinear condition. Joint predominance in the orthogonal condition differed significantly from both the collinear and the parallel conditions, with $F_{1,6} = 57.71$ ($P < 0.0005$) and $F_{1,6} = 14.43$ ($P < 0.01$) respectively. Readers may experience this effect of collinearity by fusing the rival

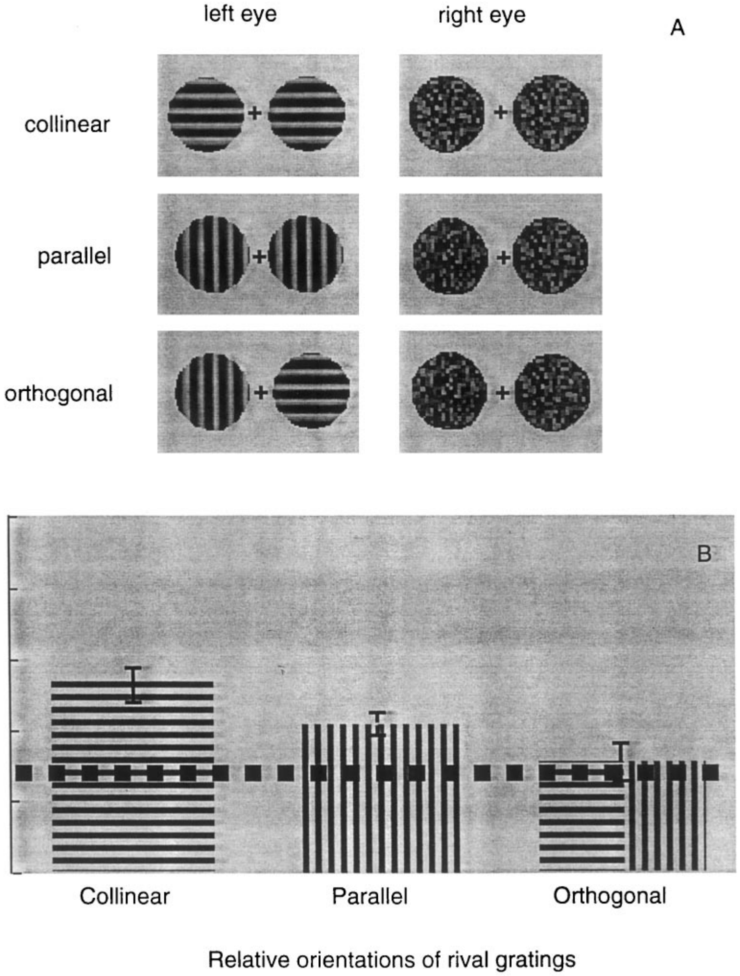

Fig. 1. Does joint predominance of two rival gratings depend on their orientations? (A) Schematic of rival target pairs used in Experiment 1. The left eye viewed a pair of sinusoidal gratings symmetrically placed with respect to a central fixation point. In one set of conditions, the two gratings were horizontally aligned (the condition shown here) and in another they were vertically aligned (not shown). From trial to trial, the orientations were collinear, parallel or orthogonal. (Note that with horizontally aligned gratings 'collinear' contours were horizontally oriented while with vertically aligned gratings 'collinear' contours were vertically aligned.) Located at corresponding areas of the right eye were two 'noise' targets that engaged in vigorous binocular rivalry with the gratings. (B) Joint predominance for collinear, parallel and orthogonal gratings; each histogram gives average data for four observers, with the error bars showing S.E. Results are for the condition where the pair of gratings were horizontally aligned; exactly the same pattern of results was obtained for vertically aligned gratings. Joint predominance specifies the amount of total dominance time that both gratings were simultaneously visible in rivalry. The horizontal, dashed line denotes the level of joint predominance predicted if the two gratings underwent independent fluctuations in dominance and suppression (estimated from trials on which only a single rival grating was presented either to the left or to the right of fixation); the thickness of this dotted line denotes the S.E. of this estimate.

targets shown in Fig. 1A and comparing joint predominance.

Does the joint predominance of collinear gratings simply reflect their contours being horizontally oriented, not necessarily collinear? To find out, we repeated the experiment with both sets of apertures now vertically aligned, centered 1.0° above and below the fixation mark. Results replicated those in Fig. 1B in all respects: collinear gratings (now both vertically oriented) exhibited significantly greater joint predominance than parallel gratings (both horizontally oriented), which in turn was greater than joint predominance with orthogonally oriented gratings. Thus, the strength of interaction in rivalry is indeed governed by good continuation defined in terms of relative orientation (collinear versus parallel versus orthogonal).

For the data shown in Fig. 1B, the two pair of rival targets were imaged in separate halves of the visual field and, hence, activated neurons in separate hemispheres. To assess the strength of grouping when both pairs of images activated the same hemisphere, we again used vertically aligned rival targets, only now with those targets imaged exclusively in one hemifield or the other. The fixation cross was repositioned laterally so that the rival targets were centered 1° to one side of the vertical midline, either in the temporal or the nasal hemifield randomly over trials. Results were qualitatively equivalent to the different hemifield conditions in that joint predominance followed the same order across orientation conditions: collinear > parallel > orthogonal. This pattern of results is consistent with the notion that similar functional organizations should exist between inter- and intra-hemispheric connections since both subserve similar functions (Innocenti, 1986; Schmidt et al., 1997). At the same time, however, we found that joint predominance was greater in the 'same hemifield' conditions, with the means (± S.E.) for collinear, parallel and orthogonal being 0.84 (±0.03), 0.78 (±0.04) and 0.38 (±0.02), respectively. Corresponding values for the different hemifield conditions (Fig. 1B) are: 0.53 (±0.05), 0.42 (±0.03) and 0.31 (±0.05). Perhaps long-range connectivity is weaker or less specific for orientation when mediated by the corpus callosum.

Joint predominance of the two gratings is expected some of the time, based on probability alone. To estimate its expected value, we measured durations of dominance and suppression for each individual grating presented alone. Over trials, this single grating appeared randomly on the left or right of fixation, either vertically or horizontally oriented. The other grating and its corresponding random dot pattern were set to 0 contrast. During 60 s trials, observers tracked fluctuations in dominance between the single grating and the corresponding noise pattern presented to the other eye. The proportion of total trial time during which a given grating dominated was calculated. The expected joint predominance value, assuming the two gratings undergo independent fluctuations in dominance and suppression, is given by the product of the relevant single grating predominance values for a particular orientation condition. Averaging over orientation and side of presentation, the expected value is 0.27 (S.E. = 0.035), indicated by the dotted black line in Fig. 1B. For the collinear and parallel conditions, the measured incidence of joint predominance exceeds that predicted by independence, implying some form of neural synergy between the jointly viewed gratings. The orthogonal condition conforms to the independence prediction.

Our data square nicely with psychophysical work by Polat and Sagi (1993, 1994) who demonstrated spatial interactions between grating patches. Using a row of three Gabor stimuli, they found that observers detected the low contrast central element more easily when high contrast flanking patches were collinear with the central target. Gabor patches with parallel orientation also facilitated detection of the central patch more than a row of Gabors with 45° orientations, suggesting a significant degree of interaction across parallel contours. This conclusion agrees with our finding that parallel orientation produced strong joint predominance. A very recent study published after completion of our work found that 'paths' of Gabor patches tended to dominate as a unit for briefly flashed, dichoptic targets (Bonneh & Sagi, 1999), an effect comparable to that found by us using conventional rival conditions. They too speculate that facilitation is mediated by lateral connections among cortical neurons.

3. Experiment 2: correlated contrast modulations and joint predominance

Besides good continuation, a second Gestalt grouping cue is 'common fate' which refers to the tendency for local elements moving in the same direction at the same speed to group perceptually into a global form (Wertheimer, 1923). (Birds flying overhead in a 'flock' represent a familiar example of this grouping principle at work.) In recent years, the concept of 'common fate' has expanded to include the tendency for spatially distributed visual features to group into coherent shapes when those features flicker on-and-off in synchrony (Fahle, 1993; Leonards, Singer & Fahle, 1996; Kojima & Blake, 1998). There is some doubt, however, about the grouping potency of synchronized flicker (Fahle & Koch 1995; Kiper, Gegenfurtner & Movshon, 1996).

Our laboratory has developed an another form of common fate that effectively promotes perceptual grouping of local features: temporal modulation in pattern contrast (Alais, Blake & Lee, 1998). On several perceptual tasks, spatially distributed grating patches undergoing changes in contrast over time tend to be seen as a single, globally coherent object when the directions of contrast change are correlated. Conversely, when the directions of contrast change are uncorrelated, the incidence of global coherence among the gratings is reduced. With respect to possible underlying mechanisms, there is reason to believe that correlated fluctuations in contrast should induce correlated changes in evoked activity within populations of neurons responsive to spatially distributed patterns (e.g. Troy & Enroth-Cugell, 1993). This, in turn, leads to the hypothesis that correlated evoked activity among populations of neurons represents a neural analog of common fate signifying spatially linked object features. Note, this hypothesis does not necessarily require that correlated neural activity take the form of temporal synchrony of individual action potentials, although there is neurophysiological evidence for just such a mechanism (e.g. Engel, König, Gray & Singer, 1990; Singer & Gray, 1995). Correlated fluctuations in modulated firing rate by themselves could also provide the requisite neural signature for grouping from contrast modulation.

Motivated by our earlier findings, we performed a second experiment to learn whether correlated contrast modulations among spatially separated rival targets promote simultaneous dominance of those targets, compared to uncorrelated modulations.

3.1. Methods

Experiment 2 employed the same observers, apparatus and procedure as Experiment 1. For this and subsequent experiments we used pairs of rival gratings imaged symmetrically to the left and right of the fixation mark (i.e. the 'different' hemifield condition). Observers generally found it easier to execute the dual tracking task with rival targets in this configuration. Stimuli for Experiment 2 were also identical to those used before, except that only horizontally aligned gratings were tested and, importantly, grating contrast was modulated in a random pattern (Fig. 2). Contrast changes were synchronized to the monitor's vertical refresh and occurred every three frames (25 Hz).

Three kinds of modulation were used: (i) correlated with equal contrasts; (ii) correlated with unequal contrasts; and (iii) uncorrelated. For correlated modulation with equal contrasts, a contrast drawn randomly from a set of seven ranging from 12 to 48% in equal logarithmic intervals was assigned to both gratings. Thus, the two gratings were perfectly correlated and underwent identical random contrast modulations. For uncorrelated modulation, two contrasts were randomly drawn from the same contrast set and assigned separately to the gratings. This ensured different grating contrasts and uncorrelated patterns of change over time between the gratings: both the amount and direction of the gratings' contrast change were independent.

Because grating contrast was always the same in the correlated conditions, and always different in uncorrelated conditions, a control condition was required in which the grating contrasts differ but contrast modulation is correlated. This constitutes the 'correlated with unequal contrast' condition and requires two contrast sets. The same log-interval separated the elements in both sets, but the set means differed by an amount equal to the average contrast difference between the gratings in the uncorrelated condition. Considering all possible pairings of grating contrast, the average difference equals 2.67 intervals. Thus, the nth element in one contrast set always differed from the nth element in the other by 2.67 intervals. Both sets were spaced symmetrically around the values in the single set conditions to ensure identical average contrast in all three modulation conditions. Thus, the higher set ranged from 16 to 65% and the lower set from 9 to 35%. The sets were randomly assigned to a grating each trial, and correlated modulations were created by assigning the nth element from both sets to their respective gratings for each contrast update. The direction of contrast change is the essential difference between conditions: either both grating contrasts increase or decrease together (correlated modulation), or grating contrasts changed independently (uncorrelated modulation). All modulations were temporally in phase, contrast changes being made during the same video retrace for both gratings.

3.2. Results and discussion

All observers gave qualitatively similar results, so data were pooled and analyzed in a two factor ANOVA. Replicating Experiment 1, the main effect of grating orientation ($F_{2,12} = 44.53$; $P < 0.0005$) was significant (Fig. 3). Planned contrasts exploring the orientation effect revealed that collinear and parallel conditions differed significantly ($F_{1,12} = 6.75$; $P < 0.05$), as did the parallel and orthogonal conditions ($F_{1,12} = 43.0$; $P < 0.001$). The new independent variable in Experiment 2 was contrast modulation. The main effect of modulation type was significant ($F_{2,12} = 40.44$; $P < 0.0005$) and strongly affected joint predominance of the gratings. Planned contrasts confirmed that joint predominance was stronger when the modulation was correlated with equal contrasts than when it was correlated with unequal contrasts ($F_{1,12} = 7.78$; $P < 0.05$), and that uncorrelated contrast modulation was much weaker than the 'correlated unequal' condition ($F_{1,12} = 36.12$; $P < 0.005$).

Comparing the histograms in 1B and 3, we see that introduction of correlated contrast modulation amplifies joint predominance relative to conditions in

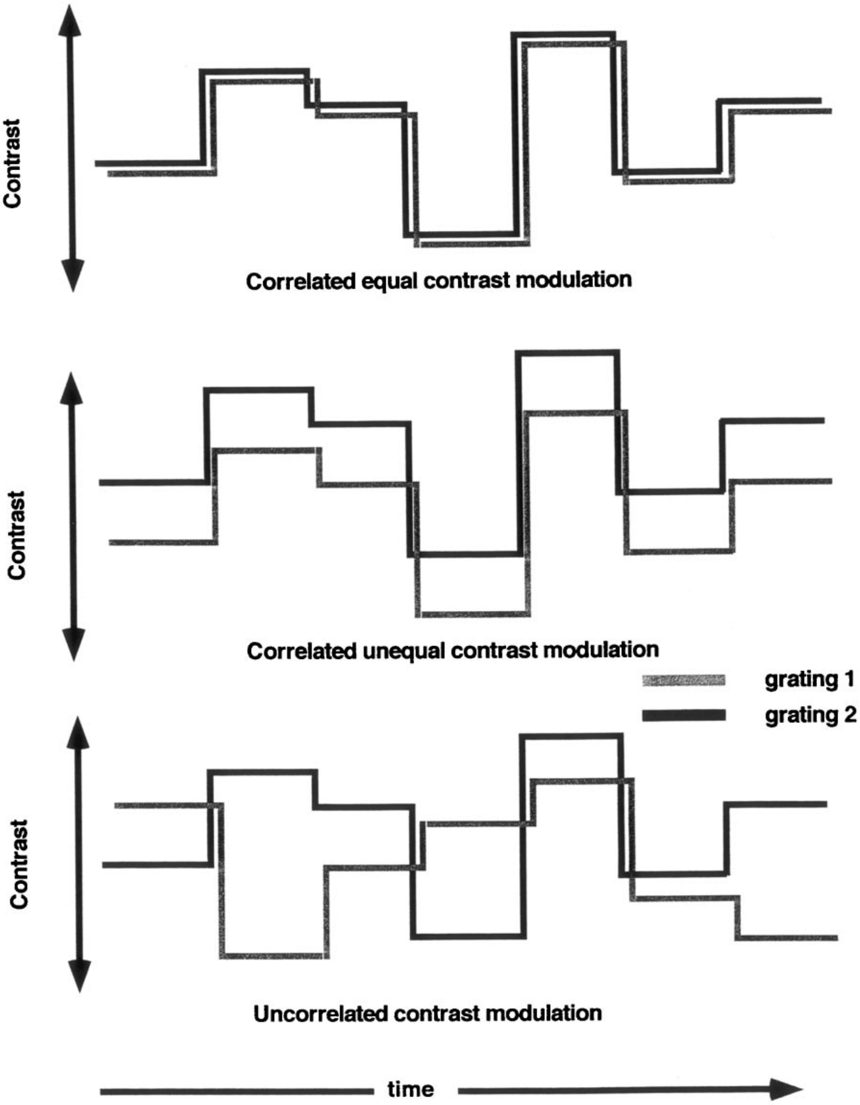

Fig. 2. Schematic showing patterns of contrast modulation for correlated and uncorrelated conditions. The contrast of a given grating changed every 39.9 ms (three video frames), with the direction and magnitude of change being pseudo-random. On trials involving correlated contrast modulations, both gratings followed identical random patterns of contrast change; on trials involving uncorrelated contrast modulations, each grating followed its own, independent pattern of change. Two types of correlated trials were administered: (i) correlated equal, wherein both gratings were identical in contrast; and (ii) correlated unequal, in which the two gratings differed in absolute contrast (by an amount equal to the average difference associated with the 'uncorrelated' condition) but followed identical patterns of change over time.

which grating contrast remains constant over time. This is consistent with our earlier finding that correlated contrast modulation promotes grouping of local elements into a globally coherent form (Alais et al., 1998), and with results showing that dynamic stimuli tend to dominate in rivalry compared to static ones (e.g. Breese, 1899; Blake, Yu, Lokey & Norman, 1998).

To estimate predominance expected on the basis of probability alone, we again collected single grating data, this time using contrast modulated patterns. Averaging over orientation and side of presentation, the expected value is 0.32 (S.E. = 0.02), indicated by the dotted black line in Fig. 3. In this case, all conditions yield joint predominance in excess of probability, even the orthogonally oriented gratings undergoing uncorrelated contrast modulations. For all grating pairs, of course, their contrasts are changing synchronously in time. Perhaps this common event is sufficient to produce some degree of interdependence in dominance, even though the direction of contrast changes are uncorrelated. We shall return to this point in a subsequent section, exploring in particular the importance of temporal coincidence in joint predominance.

Upon presenting two pairs of rival gratings to each eye, Dörrenhaus (1975) reported that two gratings of a given orientation were often simultaneously dominant even when one grating was imaged in the left eye and the other was imaged in the right eye. In a similar vein, Kovacs et al. (1997) observed that clusters of rival targets, some imaged in the left eye and others imaged in the right eye, would occasionally dominate simultaneously when those targets were identical in color or when, as a group, the cluster defined a coherent object. These observations imply that joint predominance in rivalry can arise dichoptically. To test this possibility for our stimulus configuration (which is similar to the one used by Dörrenhaus), we conducted an adjunct experiment where the positions of one grating and its corresponding random dot pattern were exchanged. Thus, the two members of the pair of gratings were presented to separate eyes, meaning that episodes of joint predominance would entail simultaneous dominance of portions of the left- and right-eyes.

Testing collinear gratings under the 'correlated with unequal contrast' and 'uncorrelated' conditions, we found that mean joint predominance (and S.E.) was 0.63 (0.02) for the 'correlated unequal' condition and 0.32 (0.02) for the uncorrelated condition. Thus like Kovacs et al. (1997), we find that the interactions promoting joint predominance can occur even with dichoptic stimulation.

3.3. Time-series analysis of joint predominance

How does correlated contrast modulation promote joint predominance between two gratings? Perhaps correlated contrast modulations boost the effective stimulus strength of the two gratings. Earlier work (Levelt, 1965; Fox & Rasche, 1969; Blake, 1977) shows that increased stimulus strength enhances predominance in rivalry by reducing the suppression of that stimulus. Thus, stronger stimuli are suppressed for shorter periods and are therefore dominant for a greater percentage of the total viewing period. It is possible, then, that correlated contrast modulations mutually strengthen the effective contrasts of the two rival gratings, thereby shortening their durations of suppression. This would have the inevitable effect of increasing the periods of their overlap during dominance. Alternatively, dominance and suppression phases associated with the two gratings may remain unchanged in duration but become temporally aligned, or phase-locked, by virtue of correlated contrast modulations.

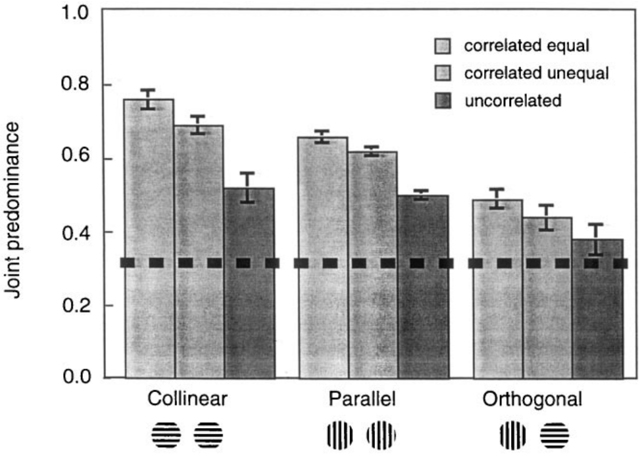

Fig. 3. Joint predominance for collinear, parallel and orthogonal gratings undergoing correlated equal, correlated unequal or uncorrelated contrast modulations in Experiment 2. Histograms give average results for four observers, with error bars denoting S.E. The dotted line denotes the level of joint predominance expected on the basis of probability alone (0.32), with the thickness of the line representing the S.E. of this estimate (0.02). These estimates were obtained from trials on which only a single rival grating modulating in contrast was presented either to the left or to the right of fixation.

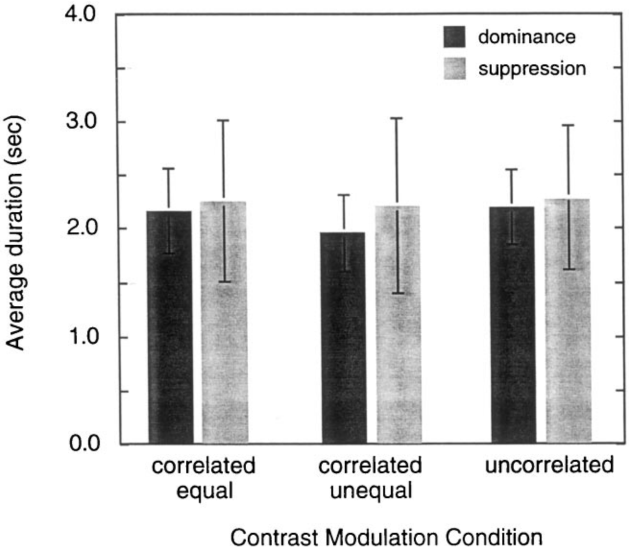

Fig. 4. Average durations of dominance and average durations of suppression for correlated equal, correlated unequal and uncorrelated conditions of contrast modulation in Experiment 2. These data come from the 'collinear' condition in which joint predominance was greatest. There is no tendency for these average durations to vary among conditions, ruling out 'stimulus strength' (see text) as an account for the increased joint predominance with correlated contrast modulations.

To evaluate these alternatives, we compared average durations of dominance and suppression for the correlated equal, correlated unequal and uncorrelated conditions. Only collinear conditions were analyzed, since they provide the greatest joint predominance and, therefore, the strongest test of the 'stimulus strength' hypothesis. As summarized in Fig. 4, these average durations reveal no tendency for suppression or dominance durations to vary with the contrast modulation conditions. Correlated contrast modulation, then, does not boost the effective stimulus strength of a given grating. This implies that enhanced joint predominance results from the temporal alignment of the alternating dominance and suppression periods of the two gratings.

To verify this implication, we performed a time series analysis (Chatfield, 1997) on the successive dominance and suppression alternations of the two gratings. Cross correlation functions between the two data sets were calculated for time lags ranging up to approximately ± two cycles of rivalry. If the gratings undergo independent fluctuations in rivalry, the correlation coefficients should vary unsystematically with phase-lag. Results for the three contrast modulation conditions (Fig. 5) show a sharp peak in correlation around zero lag, indicating a tendency for dominance and suppression durations to be aligned in time. The peak correlation value ranged from 0.3 to 0.6 over trials. No such trend was seen in any of the data sets for uncorrelated contrast modulation. This pattern of results confirms that enhanced joint predominance arises from the rivalry alternations of the two spatially separated rival targets becoming temporally aligned. There was no systematic tendency for the cross correlation peak to deviate from zero, even for the 'unequal correlated' condition where one grating had higher average contrast than the other.

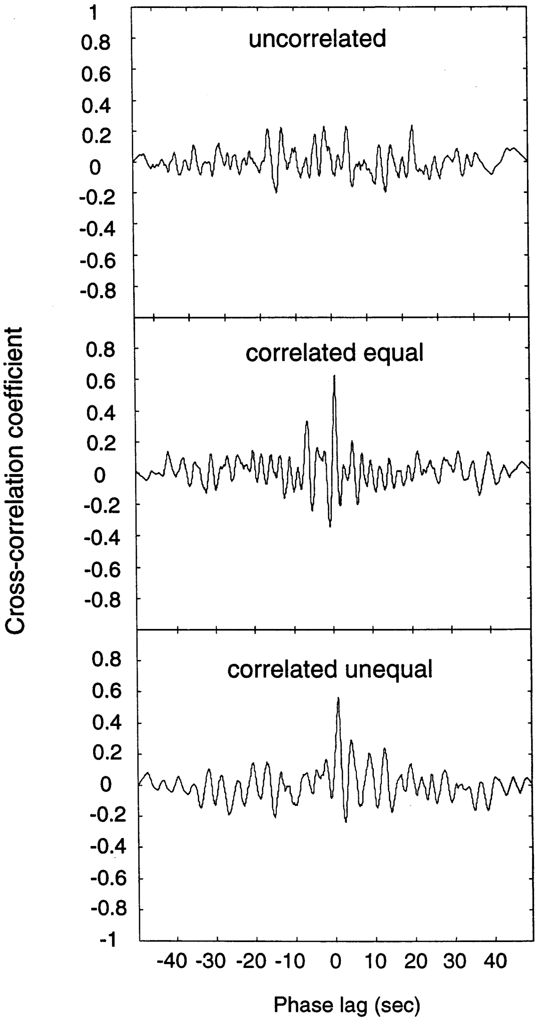

Fig. 5. Cross correlation functions for the three conditions of contrast modulation. For the two correlated conditions, the temporal dynamics of rivalry tend to become synchronized, such that periods of dominance and suppression coincide. This tendency is reflected in the relatively large, positive correlation seen around zero phase lag.

4. Experiment 3: temporal and spatial phase affect joint predominance

In the preceding experiment, contrast changes in the two gratings were exactly coincident in time, whether correlated or uncorrelated. Thus, while the direction and magnitude of contrast changes could be the same (correlated modulation) or different (uncorrelated modulation), the changes themselves were always synchronous. Does synchronized change per se promote grouping and, thus, increase joint predominance? There was some hint of this in the first two experiments: even uncorrelated contrast modulations in Experiment 2 yielded joint predominance in excess of that observed for gratings unvarying in contrast used in Experiment 1. Thus in this third experiment we examined the role of temporal coincidence by varying the temporal phase of contrast changes. We also examined the role of spatial phase on joint predominance, comparing 'correlated unequal' and 'uncorrelated' contrast modulation for gratings that were either aligned in phase or 180° out of phase.

4.1. Methods

The observers, apparatus and procedure were unchanged from the previous experiment. Horizontally aligned apertures containing collinear gratings were used, and only two modulation conditions were compared: (i) correlated with unequal contrasts; and (ii) uncorrelated. This is the most appropriate comparison because the only difference between conditions is whether or not the contrast modulation is correlated (see Section 3.1). Temporal and spatial phase were examined separately.

To create the temporal phase conditions, the two gratings were initially allocated correlated patterns of contrast change, using the 'correlated unequal' format as described earlier. Temporal phase lags of 1, 2 or 3 video frames were introduced by delaying the onset of the random contrast sequence in one grating so that it lagged behind the other. A 0-frame delay and an uncorrelated condition were also included.

For the spatial phase conditions, 'correlated unequal' and 'uncorrelated' contrast modulations were compared for gratings with 0° spatial phase difference and for gratings 180° out of spatial phase. Contrast modulations were synchronized in time.

4.2. Results and discussion

Fig. 6A shows the average data for the four observers in the temporal phase conditions. The uncorrelated

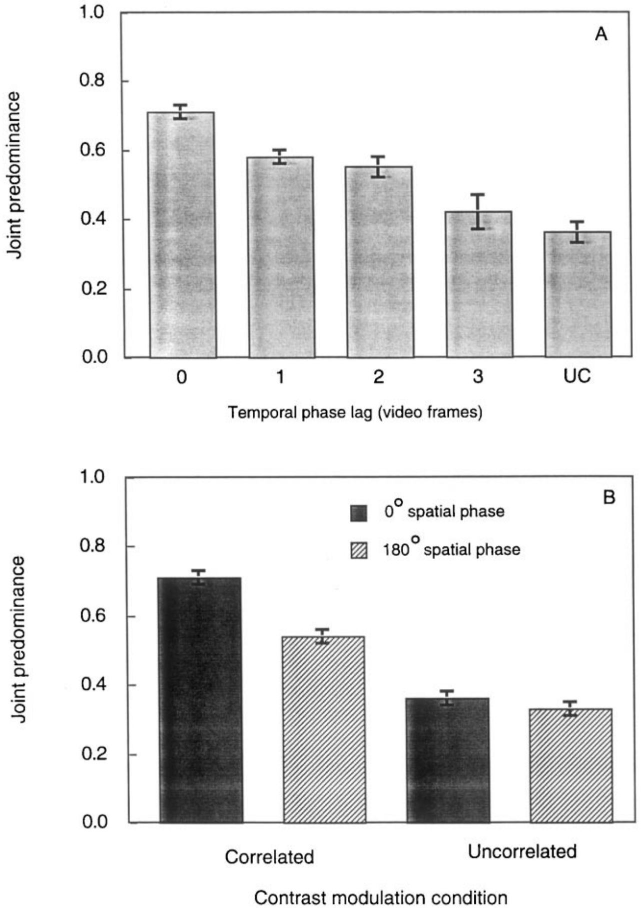

Fig. 6. Effect of temporal phase and spatial phase on joint predominance (Experiment 3). (A) Joint predominance for correlated contrast modulations in which the temporal phase of the contrast changes varied over trials. Phase lag of '0' corresponds to the 'correlated' conditions in earlier experiments. Lags of 1, 2 or 3 frames stagger the grating changes in time relative to one another. The 'UC' condition corresponds to uncorrelated contrast modulations that occurred coincident in time. (B) Joint predominance between two horizontally oriented gratings whose contours were spatially in-phase (0°) or out-of-phase (180°); contrast modulation of the two gratings was either correlated or uncorrelated. Results are averages (and S.E.) for four observers.

condition was omitted from data analysis of the four temporal lag conditions and was tested separately. A single factor ANOVA revealed significant differences among the temporal lag means ($F_{3,9} = 30.44$; $P < 0.0001$) and these were explored for linear and quadratic trend, with linear trend being significant ($F_{1,9} = 87.62$; $P < 0.0001$). Temporal lag between otherwise identical contrast modulation sequences strongly affected joint predominance. Finally, a t-test was used to compare the difference between the uncorrelated condition and the three-frame temporal lag. These conditions did not differ significantly ($t_6 = 0.97$; $P > 0.05$), indicating that synchronous change per se is not responsible for the very small boost in joint predominance produced by uncorrelated modulation (Experiment 2) relative to static, unmodulated contrast (Experiment 1). Evidently flicker itself is sufficient to convey at least a weak sense of 'common fate'. It remains to be learned whether pairs of rival targets must be flickering at equivalent rates for them to mutually interact.

Turning next to the spatial phase condition, average data for these conditions are presented in Fig. 6B. The main effect of spatial phase was statistically significant ($F_{1,3} = 20.85$; $P < 0.05$) and interacted with modulation type ($F_{1,3} = 23.15$; $P < 0.05$). Planned contrasts explored the phase effect separately for each modulation type. Spatial phase had no effect on joint predominance in the uncorrelated condition ($F_{1,3} = 0.88$; $P > 0.05$) but did in the correlated condition ($F_{1,3} = 59.95$; $P < 0.005$). Still, spatial phase's effect on joint predominance is rather modest compared to other effects documented in this paper, which is not too surprising in view of other results. Field et al. (1993) found that detection of a smooth string of Gabor patches among a background of 'noise' Gabors was unaffected by random phase variations. Polat and Sagi (1993) studied spatial interactions using a row of Gabor patches and found little effect of phase unless the patches were overlapping. Together, these results suggest that the phase sensitivity of long-range interactions among cells responding to grating patches is not great.

5. Experiment 4: spatial separation affects joint predominance

Fluctuations in dominance of spatially separated rival gratings tend to become entrained when those gratings exhibit good continuity (collinearity) or common fate (correlated contrast modulation). We believe that these cooperative effects could be mediated by long-range horizontal connections among cortical cells. In area V1 these connections span at least several millimeters and, relative to receptive field sizes, they mediate interactions roughly an order of magnitude larger than the 'average' receptive field dimension for neurons representing a given retinal eccentricity (Gilbert & Wiesel 1983; Rockland & Lund 1983; Das & Gilbert 1995). To the extent that these lateral connections play a role in the promotion of joint predominance, we would expect the angular separation of two rival gratings to influence correlated contrast modulation's power to augment joint predominance.

5.1. Methods

Observers, apparatus and procedure were as described above. Again, only the 'correlated with unequal contrasts' and 'uncorrelated' conditions were compared. The stimuli differed in that the gratings and their rival stimuli were moved into the periphery along the horizontal meridian in steps of 1.0°, symmetrically around fixation. The gratings and random dot stimuli were magnified to equate visibility across eccentricity according to the formula:

$$F = 1 + (E/E_2)$$

where F is the magnification factor, E is stimulus eccentricity, and E_2 is the eccentricity at which magnification has changed by a factor of two. E_2 was estimated at 2.6°, based on psychophysical data (Westheimer, 1982; Levi, Klein & Aitsebaomo, 1985) and physiological data (Rolls & Cowey, 1970; Dow, Snyder, Vautin & Bauer, 1981). Stimuli were horizontally aligned and centered at eccentricities of 1.0, 2.0, 3.0° either side of fixation, so overall separation was twice this distance. The number of grating cycles within the apertures was the same (five cycles) for all eccentricities, resulting in spatial frequencies of 3.33, 2.59 and 1.66 c/deg and apertures subtending 1.5, 1.93 and 3.02°.

5.2. Results and discussion

Data were pooled over observers and are shown in Fig. 7. As revealed by a two factor ANOVA, the main effects of modulation type and of eccentricity were both significant ($F_{1,3} = 73.17$; $P < 0.005$ and $F_{2,3} = 23.49$; $P < 0.005$ respectively), and both variables interacted strongly ($F_{2,6} = 77.72$; $P < 0.0001$). The expected drop in joint predominance with eccentricity in the correlated condition was explored with planned contrasts testing for linear and quadratic trends. These indicate that the fall-off is linear rather than quadratic ($F_{1,2} = 101.37$; $P < 0.001$ and $F_{1,2} = 3.53$; $P > 0.05$ respectively). Importantly, the reduced joint predominance with eccentricity does not arise from an overall reduction in grating dominance. Total dominance duration was essentially invariant with eccentricity, averaging 32, 30 and 30 s (average S.E.: 2.6 s) in the correlated conditions, and 31, 29 and 30 s (average S.E.: 2.6 s) in the uncorrelated conditions. Knowing that predominance varies with stimulus visibility, these data confirm that the magnification scaling procedure effectively equated visibility with eccentricity.

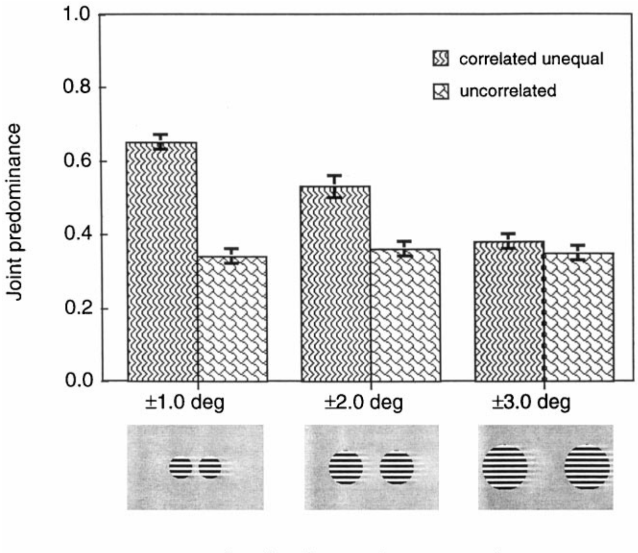

Fig. 7. Joint predominance for gratings differing in center-to-center distance (Experiment 4). Both gratings were centered horizontally about a central fixation point, and the angular sizes and spatial frequencies were scaled for cortical magnification (see text for details). Results are averages for four observers; error bars give S.E.

Thus correlated contrast modulation's efficacy in promoting joint predominance has limited spatial extent, as expected. In area V1 lateral connections mediate interactions roughly an order of magnitude larger than the average receptive field dimension for a given eccentricity. Taking into account the eccentricities we tested, our data showing no interactions beyond 4° separation is in reasonable agreement with this scale factor.

6. Experiment 5: linking spatially remote rival targets

Because of good continuation, a pair of closely spaced, collinear rival gratings can be construed as two visible portions of a single, partially occluded textured object (see, for example, the collinear grating pair in Fig. 1A). Thanks to common fate, correlated contrast modulation of those visible portions reinforces that impression. Evidently, however, good continuation and common fate are restricted to visual features in relatively close proximity, as implied by the results from Experiment 4. Beyond some upper limit the two visible portions of the array behave as separate entities, each fluctuating in dominance entirely on their own. Could this upper limit be extended by inserting a third pattern mid-way between the two gratings? Based on the principles of good continuation and common fate, an effective linking pattern would need to be collinear with the flanking gratings and would need to undergo contrast modulations that were correlated with them. Experiment 5 tests the necessary conditions for extending the spatial extent of joint predominance.

6.1. Methods

Observers, apparatus and procedure were the same as those used for Experiment 4. The rival targets were horizontally aligned 3° to either side of central fixation, and the aperture diameter (3.02°) and spatial frequency (1.66 c/deg) were appropriately scaled for that eccentricity. Situated midway between the two rival gratings was a third 'linking' grating identical in size and spatial frequency to the rival gratings. The linking grating had no rival target imaged on the corresponding area of the other eye (which was set to the average luminance), thus it was always visible. Three conditions were tested: (i) the horizontal flanking gratings and a horizontal linking grating all underwent 'correlated unequal' contrast modulations (collinear/correlated); (ii) horizontal flanking gratings underwent correlated contrast modulation while a horizontal linking grating underwent independent contrast modulation (collinear/uncorrelated); (iii) the horizontal flanking gratings and a vertical linking grating all underwent 'correlated unequal' contrast modulations (orthogonal/correlated). Observers tracked periods of dominance of the two flanking gratings while maintaining fixation on a small cross centered on the linking grating.

6.2. Results and discussion

Pooled data are shown in Fig. 8. The large difference between the collinear /correlated and the collinear/uncorrelated conditions was significant ($t_6 = 21.43$; $P < 0.0001$) but the difference between the orthogonal/correlated and the collinear/uncorrelated condition was not significant ($t_6 = 1.19$; $P > 0.05$). Thus a linking grating that reinforces good continuation and common fate can reestablish joint predominance of two rival targets that are otherwise beyond the spatial range of interaction.

7. Conclusions

Binocular rivalry provides a promising means for studying links between neural events and perceptual events. During rivalry a given stimulus disappears for seconds at a time from visual awareness, even though that stimulus remains imaged on the retina. We would expect to find correlated fluctuations in neural activity associated with the intermittent disappearance of that stimulus, and even now the search for those neural correlates is successfully underway (Logothetis & Schall, 1989; Leopold & Logothetis, 1996; Fries, Roelfsema, Engel König & Singer, 1997). Moreover, rivalry seems to operate within local spatial zones that may correspond to receptive fields of neurons organized in hypercolumns (Blake et al., 1992). Dominance among local zones can become coordinated, however, yielding joint predominance of spatially distributed object features (Kovacs et al., 1997; Alais & Blake, 1998). Here, too, there should exist neural signatures of this phase-locked behavior. The present experiments reveal potent roles for common fate and good continuation in perceptual grouping during binocular rivalry, thereby providing potentially helpful clues about possible neural bases of visual grouping.

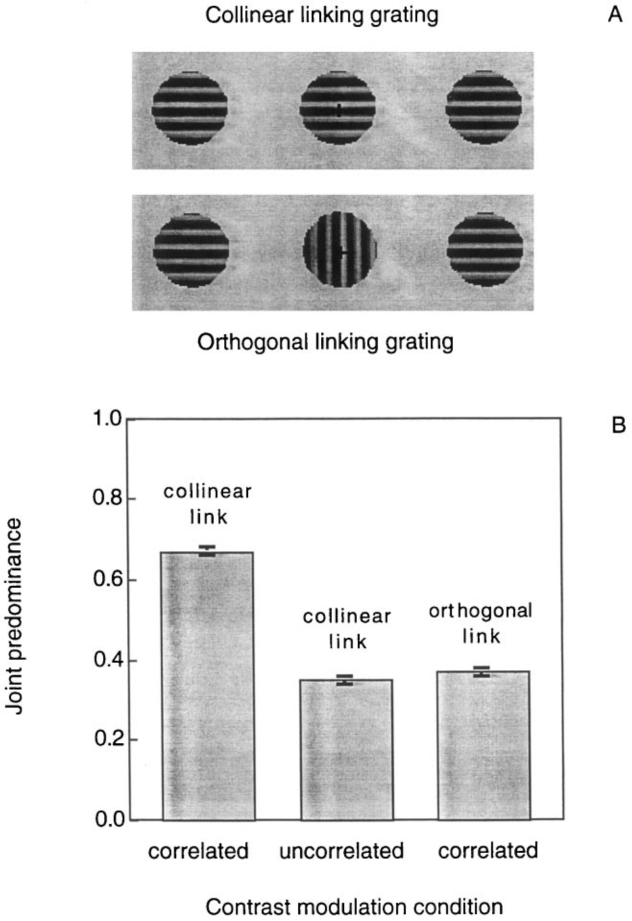

Fig. 8. Restoration of joint predominance between two widely separated rival gratings (Experiment 5). (A) Two collinear gratings were separated by 3.0° (6.0° center-to-center distance), a separation too large to promote joint predominance (see Fig. 7). A third 'linking' grating was placed midway between the two rival gratings, at the point of fixation, and its contours were either collinear or orthogonal with respect to the horizontal contours of the two rival gratings. The two rival gratings underwent correlated modulations in contrast, and the 'linking' grating underwent either correlated or uncorrelated contrast modulations relative to the rival gratings. There was no pattern located at the corresponding area of the right eye-the 'linking' grating was visible continuously. (B) Joint predominance for the two rival gratings as the function of the similarity in orientation and in contrast modulation between rival gratings and 'linking' grating.

To reiterate, our results show that pairs of collinear rival gratings exhibit exceptionally strong joint predominance, suggesting the possible involvement of long-range intrinsic connections in visual cortex (Ts'o & Gilbert 1988; Ts'o et al., 1986; Schmidt et al., 1997). Moreover, this joint predominance decreases with lateral separation between rival gratings, which also parallels variations in connection strength with cortical distance. Correlated contrast modulation between two rival gratings also encourages joint predominance of the two, by temporally aligning their successive dominance durations. It is tempting to think about this synergistic effect in terms of correlated fluctuations in activity among ensembles of neurons responsive to the two patterns (cf Li, 1998). But, in fact, the actual consequence of correlated contrast modulation on distributed cortical responses cannot be known until these kinds of stimuli are utilized in neurophysiological experiments. We hope future collaborations will be directed toward this end. Meanwhile, the present results validate the usefulness of binocular rivalry as a tool for studying perceptual grouping.

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