Contour interactions between pairs of Gabors engaged in binocular rivalry reveal a map of the association field

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Abstract

A psychophysical study was conducted to investigate contour interactions (the 'association field'). Two Gabor patches were presented to one eye, with random-dot patches in corresponding locations of the other eye so as to produce binocular rivalry. Perceptual alternations of the two rivalry processes were monitored continuously by observers and the two time series were cross-correlated. The Gabors were oriented collinearly, obliquely, or orthogonally, and spatial separation was varied. A parallel condition was also included. Correlation between the rivalry processes strongly depended on separation and relative orientation. Correlations between adjacent collinear Gabors was near-perfect and reduced with spatial separation and as relative orientation departed from collinear. Importantly, variations in cross-correlation did not alter the rivalry processes (average dominance duration, and therefore alternation rate, was constant across conditions). Instead, synchronisation of rivalry oscillations accounts for the correlation variations: rivalry alternations were highly synchronised when contour interactions were strong and were poorly synchronised when contour interactions were weak. The level of synchrony between these two stochastic processes, in depending on separation and relative orientation, effectively reveals a map of the association field. These association fields are not greatly affected by contrast, and can be demonstrated between contours that are presented to separate hemispheres.

1. Introduction

The primary visual cortical area (V1) contains neurons that are specialised for the detection of stimuli that are narrowband in orientation and spatial frequency. V1 also has the finest spatial grain of all visual cortical areas, with receptive field sizes on the order of 1°–2° diameter, and considerably less in the fovea. With the visual field spanning more than 180°, orientation information must be pooled across V1 units if contours are to be signalled on all but the most local scale. In the recent decade or so, neurophysiological research has revealed a rich network of long-range connections in V1 which suggest localised edge detectors may be organised into larger networks dedicated to signalling long contours in the retinal image. A large literature has emerged detailing the patterns and nature of these connections (Angelucci & Bullier, 2003; Series, Georges, Lorenceau, & Fregnac, 2002). Briefly, neurons of a given orientation selectivity are preferentially connected to others with a similar orientation preference and adjacent receptive fields (Hirsch & Gilbert, 1991; Schwarz & Bolz, 1991; Stettler, Das, Bennett, & Gilbert, 2002; Ts'o, Gilbert, & Wiesel, 1986; Weliky, Kandler, Fitzpatrick, & Katz, 1995). These connections can span up to 5 mm of cortical distance in primates (Angelucci et al., 2002) and the connective density of these long-range (LR) intrinsic connections is elongated along the iso-orientation axis (Chisum, Mooser, & Fitzpatrick, 2003; Hirsch & Gilbert, 1991; Malach, Amir, Harel, & Grinvald, 1993; Schwarz & Bolz, 1991; Weliky et al., 1995). It is thought that this pattern of connectivity subserves the

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extraction of extended (and potentially fragmented) contours from the retinal image as early as V1, which is necessary for image segmentation and assignment of object boundaries, and consequently depth ordering and object formation (Geisler, Perry, Super, & Gallogly, 2001).

In tandem with these advances in V1 neurophysiology, there has been a burgeoning psychophysical literature demonstrating the relatedness of discrete contour elements in perceptual tasks. Two papers have been seminal in the proliferation of psychophysical contour interactions. In one, (Field, Hayes, & Hess, 1993) demonstrated the role of orientation-tuned lateral interactions in the detection of extended contours within larger arrays of randomly oriented noise elements. They coined the term 'association field' to describe the propensity of oriented elements to group with neighbouring elements of similar orientation and spatial location and thus stand out from the background of noise elements. They found that long sequences of adjacent Gabors could integrate into smooth global contours provided spatial separation was small ($\leqslant 6$ carrier wavelengths (λ)[1]) and the orientation difference between elements was not great ($\leqslant 30°$). In the other key paper, (Polat & Sagi, 1993) introduced the lateral masking paradigm and showed that detection of a Gabor patch could be facilitated when flanked by Gabors of similar orientation. Detection facilitation was maximal for flanking stimuli that were spatially proximal (separations of $2–3\lambda$) and oriented collinearly with the target. Several studies have confirmed Polat and Sagi's basic finding that detection facilitation decreases as the target and flankers vary from collinear (Kapadia, Ito, Gilbert, & Westheimer, 1995; Williams & Hess, 1998), although others have demonstrated significant target facilitation also occurs when flankers are oriented orthogonally to the target (Cass & Spehar, 2005b; Yu, Klein, & Levi, 2002).

In this paper, we seek to map the association field using a novel psychophysical method. Our motivation comes from limitations associated with the two methods just mentioned. In the path detection paradigm favoured by the Hess group, the role of the surrounding noise elements is to mask the detection of the suprathreshold global contour which otherwise would be trivially easy. This allows the performance limits of global contour detection to be investigated, although a negative consequence of using orientation noise to mask the target contour is that it impinges on the very relationship being measured. For any element in the global contour, the probability of a false (non-target) association being formed with a neighbouring noise element increases with path curvature. Curvature limits for effective contour integration obtained with the path detection paradigm may therefore be limited by this artificial ceiling effect. The data we report below, obtained without

surrounding orientation masks, reveal strong associations between elements oriented well beyond 30°. Polat and Sagi's lateral masking paradigm is not limited by the masking constraint, although it does have the drawback of being a threshold detection task and it is not necessarily indicative of contour integration at suprathreshold contrast levels (Hess, Dakin, & Field, 1998).

To overcome the limitations of the path detection and the lateral masking approaches, a paradigm is required in which lateral interactions occur at high-contrast and unhindered by noise elements. In the simplest case, lateral interactions would be studied between just two, high-contrast contour elements. Here, we present such a paradigm, using local binocular rivalry as a tool. In binocular rivalry, conflicting monocular targets are presented to the eyes, provoking a binocular competition in which the monocular stimuli are alternately suppressed, so that only one is visible at a time (Alais & Blake, 2005). Visibility of a given target typically lasts only a second or so, after which it becomes suppressed so that the stimulus in the fellow eye becomes dominant. This alternation of monocular dominance continues irregularly for as long as the conflicting stimuli are present.

Binocular rivalry, especially between simple contoured elements, is thought to be a local and low-level competition between monocular channels (Blake, 1989; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). The local nature of the rivalry processes is evidenced by the fact that large rivalling stimuli do not alternate wholly, but in a piecemeal fashion such that many rivalry processes occur simultaneously in small local regions. The small size of these rivalry zones suggests a low-level process with small receptive fields. Indeed, rivalry zones in central vision are roughly the size of V1/V2 receptive fields and they increase in size with eccentricity according to the V1/V2 magnification function (Blake, O'Shea, & Mueller, 1992). Provided the competing stimuli are smaller than this function specifies, the binocular rivalry process will be essentially binary: either one stimulus or the other dominates, with piecemeal rivalry not observed. When larger stimuli engage in binocular rivalry it is sometimes observed that the suppressed stimulus first becomes visible in a local region and then spreads across the image along a wave-like front. This kind of behaviour suggests that there must be links between adjacent rivalry processes, perhaps mediated by long-range intrinsic connections (Alais & Blake, 1999), since emergence from suppression in one local zone tends to prompt neighbouring zones to break suppression (Lee, Blake, & Heeger, 2005; Wilson, Blake, & Lee, 2001) and since good continuation also plays a role in generating coherent rivalry alternations in larger stimuli (Lee & Blake, 2004).

The aim of the present paper is to describe the links between local binocular rivalry processes. Two small Gabor patches in one eye each rival with random-dot patches in the fellow eye. Observers track the alternations in dominance and suppression for each Gabor with key presses, and the two time series are cross-correlated. Relative

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[1] More recent experiments indicate that that contour integration performance is less dependent upon 'path' inter-element separation (75% up to $7–10\lambda$ separation) (Hess, Hayes, & Field, 2003) if one equates signal (path) and noise (distractors) inter-element separation.

orientation is varied smoothly from collinear through oblique to orthogonal and the spatial separation of the elements is also varied. The degree of cross-correlation provides a measure of association strength between the two processes. Because the rival stimuli are small oriented patches, this paradigm should reveal the association strengths between orientation-selective V1 units. Indeed, consistent with the 'association field' proposal, we find that rivalry sequences for adjacent collinear Gabors are very highly correlated, less so for widely separated collinear Gabors, and least for orthogonally orientated Gabors. By measuring rivalry correlations for a matrix of spatial separations and relative orientations, we are able to derive a topography of lateral interactions—a map of the association field-obtained at suprathreshold contrast between just two elements without the presence of masking noise.

2. Experiment 1

The first experiment examines the strength of association between rivalling, high-contrast Gabor patches as a function of separation and relative orientation, at three spatial frequencies (2, 4, and 8 cpd). If two Gabor patches engaged in local binocular rivalry do indeed interact according to the association field hypothesis, then the expected pattern of results is for strongly cross-correlated rivalry alternations for adjacent and collinear Gabor patches, falling off with spatial separation and increasing relative angle. To preview the results, effects of orientation and separation are indeed found, and this leads to a subsequent analysis examining the binocular rivalry data to determine whether variations in association strength have an impact on the binocular rivalry process.

2.1. Methods

2.1.1. Subjects

Four observers participated in this experiment. All had normal or corrected-to-normal vision.

2.1.2. Stimuli and apparatus

The stimuli (depicted in Fig. 1A) were generated on an Apple Macintosh G4 computer using Matlab software in conjunction with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) and presented on a γ-corrected Sony SE II video monitor running at 100 Hz vertical refresh rate. The left and right eyes' stimuli were presented on the screen simultaneously and viewed dichoptically through a mirror stereoscope. The total distance from the screen to the eyes (including the stereoscope) was 114 cm. The right eye viewed a pair of Gabor stimuli while the left viewed a pair of random-dot patches in corresponding locations. Each pixel in the random dot patch was set to a random luminance level and the patch was windowed by the same Gaussian envelope as the Gabor patches. In separate blocks, the Gabors had carrier frequencies of 2, 4, or 8 cpd and the Gaussian envelope was scaled so that there were
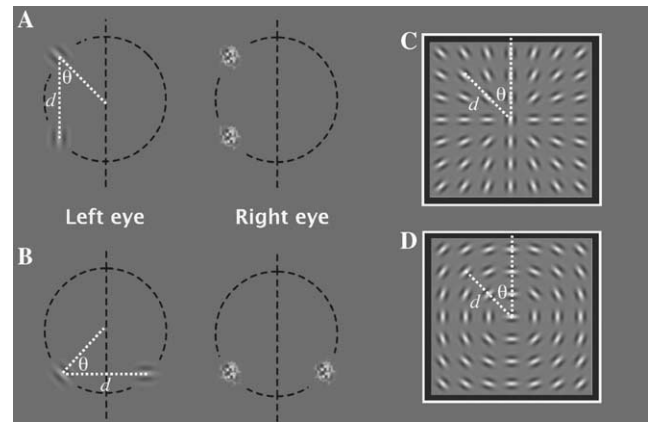

Fig. 1. Illustrations of the stimuli used in these experiments. (A) Two Gabor patches were presented to one eye and were located on a virtual circle with a radius of 6λ centred on a fixation point. In Experiments 1 and 2, both Gabors appeared on one side of the vertical mid-line, ensuring that they activated the same cerebral hemisphere. In corresponding locations in the fellow eye, patches or random visual noise were presented, causing the Gabors and the noise patches to engage in binocular rivalry. The observers task was to monitor continuously the appearance and disappearance of the two Gabor patches, and the two resulting time series were cross-correlated to measure the degree of association between the rivalry alternations. (B) In Experiment 3, the two Gabors were presented either above or below the horizontal mid-line of the virtual circle (and astride the vertical midline), so that they would activate different cortical hemispheres. Again, noise patches were presented to the fellow eye and the two resulting rivalry processes were tracked over time and their association strength obtained by cross-correlating the two time series. (C) The two Gabors on the virtual circle had a relative orientation and centre-to-centre separation that was drawn from this matrix (see Section 2.1). The idea was to map the topography of the association field by presenting the centre element (shown by the bold square) on all trials and pairing it with another chosen randomly from the surrounding elements (shown by the dashed square). Once selected, the Gabor pair was presented at a random position on the virtual circle but with the same spatial separation and relative orientation as in the matrix. Presenting the stimuli in the circle format maintained a constant retinal eccentricity (always 6λ), avoiding counfounds due to changing receptive field size and association strength with eccentricity. (D) Similar to (C), except that all orientations (excluding the central element) have been rotated by 90°. This creates a parallel condition (in place of the orthogonal) and also an oblique condition that is concave. Oblique concace is not consistent with smooth boundary closure, as opposed to the oblique convex condition in (C) (Kellman & Shipley, 1991).

always 1.5 carrier cycles visible at the full-width half-height. The screen area beyond the stimuli was set to average luminance (32.7 cd/m²) and the contrast of the Gabors and the random-dot noise patches was 100%.

The two key parameters in the experiment are the spatial separation and relative orientation of the two Gabors. These were chosen randomly from trial to trial from the 7*7 matrix of combinations shown in Fig. 1C. The central Gabor was used for all trials and it was paired with a randomly drawn element from the surrounding matrix on a given trial. Cells in the matrix were separated by a distance of 2.5λ, and all surrounding cells were oriented to 'point' to the centre cell. Once selected from the matrix, the pair of stimuli were spatially transformed so that they could be

presented on the perimeter of a virtual circle with a radius of 6λ centred on the fovea. The reason for this was to keep stimulus eccentricity constant, since both receptive field size and the strength of lateral interactions among contours are known to vary with eccentricity (Hess & Dakin, 1997; Hess & Dakin, 1999; Nugent, Keswani, Woods, & Peli, 2003). For the purposes of our experiment, the matrix and the circle formats can be made equivalent in terms of the two key parameters, relative orientation and spatial separation. That is, a pair of elements can be located on the circle and then spaced around the perimeter by an amount that will produce the same separation as exists between the two Gabors in the matrix. Once appropriately spaced apart, the elements can each be locally rotated to reproduce the same relative orientation as specified in the matrix. Thus, the two formats are essentially equivalent, although the circle format has the advantages that: (i) the stimuli are always equi-peripheral, precluding eccentricity confounds as separation varies, and (ii) the stimulus pair can be offset randomly around the circle from trial to trial to avoid adaptation building up over trials in the same spatial locations. Note that in Experiment 1, the Gabor pairs were always located on the right-hand half of the virtual circle so that the rivalry processes would take place between nearby columns within the same cerebral hemisphere (to better reveal the pattern of local association effects).

2.1.3. Procedure

Observers viewed the two pairs of rivalling stimuli for 60 s periods. Their task was to track the rivalry alternations in both stimuli by pressing one key when one Gabor was visible, and another key when the other Gabor was dominant. The two resulting time series were then analysed in several ways. First, they were cross-correlated to obtain a measure of the degree of association strength between the two rivalry processes. Second, the average duration of the dominance and the suppression periods was calculated for each process. The cross-correlation value was then entered into a 7*7 data matrix in the position of the surrounding cell, representing the association strength between the grating in that position and the one in the central position. The 60-s tracking periods were conducted five times for each cell and the five values were averaged and standard errors obtained. When complete, the data matrix can be plotted as a surface representing the association field (see Fig. 2A) or the data along the collinear, orthogonal and oblique axes can be plotted (Fig. 2B). In practice, it was sufficient to measure just one quadrant of the matrix and duplicate it to complete the map as association fields are symmetrical (and pilot data showed no differences between quadrants). Five measures were made of each of the 15 pairings within a quadrant.

2.2. Results

2.2.1. Association field data

Association field maps obtained at three different spatial frequencies (2, 4, and 8 cpd) are shown in Fig. 2A. These plots are interpolations of raw data which have been smoothed using a Gaussian filter kernel with a standard deviation of
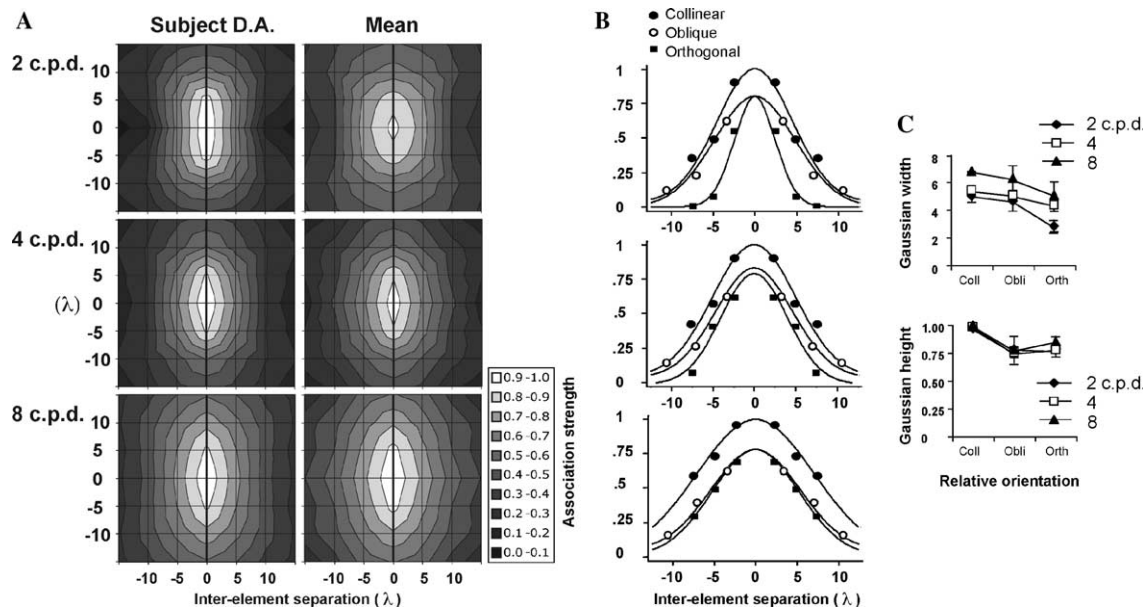

Fig. 2. Association strength data from Experiment 1. (A) Surface plots of the association field implied by the cross-correlation data of Experiment 1, shown here for 3 spatial frequencies. To obtain the surface plot, the association strength for each cell in the matrix shown in Fig. 1C (when paired with the centre element) was plotted in a 7*7 matrix, and the data interpolated and smoothed (using a Gaussian filter kernel with a width of 1.5λ to remove jagged edges). This surface therefore represents the association field around a vertically oriented Gabor located in the centre of the plot (as in Fig. 1C). In practice, it was sufficient to measure just one quadrant of the matrix and duplicate it to complete the map as association fields are symmetrical. (B) Best-fitting Gaussians fitted to the collinear, oblique and orthogonal dimensions of the (unsmoothed) mean data from Experiment 1, shown separately for spatial frequencies of 2, 4, and 8 cpd (from top to bottom). (C) The amplitudes and half-bandwidths at half-height for the best fitting Gaussians shown in (B).

1.5λ to remove jagged edges from the iso-association contours. The spatial separation between Gabors is represented in units of carrier wavelength (λ). The maps therefore have a greater spatial extent in terms of absolute distance as spatial frequency decreases, however they are all roughly congruent and self-similar when plotted in terms of wavelength. This agrees with other psychophysical data (Cass & Spehar, 2005a; Dakin & Hess, 1998; Polat & Sagi, 1993; Woods, Nugent, & Peli, 2002). Our data are therefore consistent with these findings and support the claim that patterns of intrinsic connections are self-similar when plotted in terms of wavelength despite spanning different cortical distances proportional to the wavelength of their spatial frequency preference.

The shapes of the association fields also appear very similar across spatial frequency, in that associations extend further in the collinear direction than in the orthogonal direction at all frequencies. There appears to be a tendency for the association fields to become slightly rounder as frequency increases (see Fig. 2B). This is reflected in the aspect ratios of the association field maps reducing towards unity as spatial frequency increases. The aspect ratio is the standard deviation of the Gaussian fits for the collinear dimension (weighted by the amplitude of the collinear Gaussian) divided by the standard deviation of the orthogonal dimension (weighted by the amplitude of the orthogonal Gaussian), which yields values of 2.14, 1.57, and 1.50 for the spatial frequencies of 2, 4, and 8 cpd, respectively (aspect ratios greater than 1 indicate an association field map elongated in the collinear dimension). In all cases, cross-correlations are strongest at the smallest spatial separation and falls off as separation increases. Interestingly, even though cross-correlations were strongest between collinear Gabor patches, there is no relative orientation at which significant associations are not possible. This is true even for orthogonally oriented contours, particularly when they are adjacent. Instead, association strength appears to depend on an interaction between relative orientation and spatial separation such that strong associations between collinear elements can occur over relatively large separations while orthogonal elements will only associate strongly over short separations. It is this interaction that accounts for the association field having a longer extent in the collinear dimension than in the orthogonal dimension.

The reductions in cross-correlation with increasing spatial separation is well described by a Gaussian function. Fig. 2B shows the best-fitting Gaussians through the collinear, orthogonal and oblique dimensions of the data (i.e., relative orientations of 0°, 90°, and 45°, respectively). The two free parameters in the fits are the amplitude and the width (sigma) of the functions. Amplitude provides an index of the main effect of orientation on association strength and is greatest for the collinear fit, less for the oblique fit, and least for the orthogonal fit. The width of the fits provides an index of the spatial extent of association. Associations extend furthest in the collinear direction and least in the orthogonal dimension, with oblique associations having an intermediate spatial range.

2.2.2. Binocular rivalry data

An interesting question as far as the rivalry data is concerned is whether the average dominance duration of a Gabor patch engaged in rivalry varies as a function of association strength. The interesting outcome is that no change at all is observed in the dominance durations of the two Gabors. Fig. 3A shows that the average dominance durations at all separations and relative orientations were very similar and exhibit no systematic relation to the variations in strength of association. This rules out the possibility that the two Gabors were more highly correlated simply because their periods of visibility (dominance) increased so that both were visible more often (by mutual facilitation). Instead, what explains the variations in association strength as a function of angle and separation is that the two rivalry processes become synchronised in their stochastic alternations (rather than varying in dominance or suppression durations). The varying degrees of synchronisation between the rivalry processes can be seen in Fig. 3B where the time series of the two rivalry processes are plotted at two levels of association strength (top panel: 2.5λ, collinear; bottom panel: 7.5λ, orthogonal). Even though the top and bottom panels represent the conditions of maximum and minimum correlation, the average of the 'on' phases in each condition are very similar (see Fig. 3A). By contrast, the obvious change between these conditions is the degree of correlation, which is high for the top panel and low for the bottom panel.

2.3. Discussion

How does this pattern of associations between oriented elements relate to those obtained with the other methods outlined in the Section 1? Overall, it is clear that these results are broadly consistent with the findings from the both the lateral masking and the path detection paradigms in that (i) association strength is strongest for collinear alignments and falls off monotonically as relative orientation increases, and that (ii) association strength falls off monotonically with separation. Looking more closely at the data, one striking point that emerges is the reduction in association strength with relative orientation does not reach zero, even for orthogonal elements separated by 7.5λ. The original conception of the association field was that there was an orientation limit beyond which associations did not occur. This was stated as being 60°, although clearly the path identification task was already very difficult at 30° (Field et al., 1993). The fact that association strength in our experiment did not reach zero even for orthogonal elements lends credence to the suggestion that the background elements in path detection stimuli provide false matches and therefore artificially restrict the possible orientation range of contour interactions. Without background elements, our data reveal relatively strong facilitative interactions are not precluded from occurring between orthogonal contours. However, the association fields plotted in Fig. 2A suggest that strong associations exist between orthogonal elements
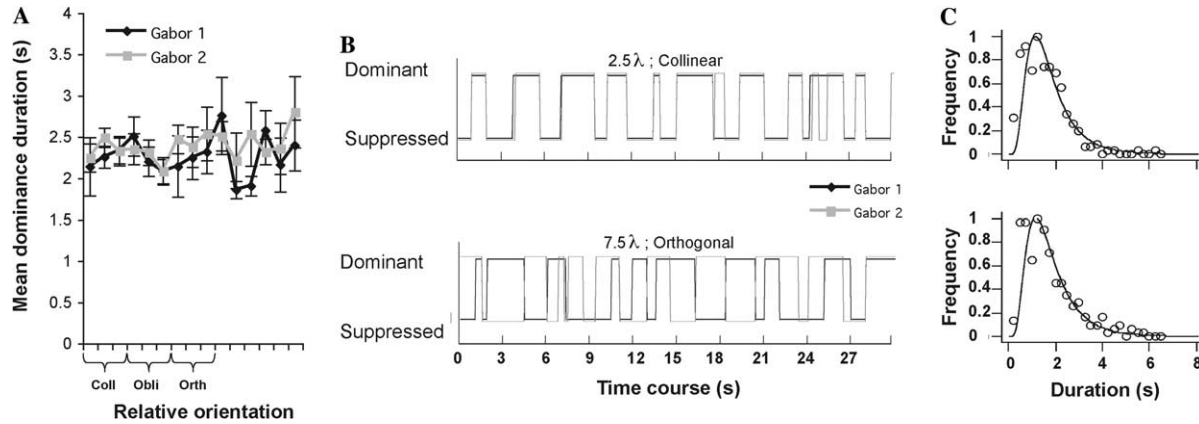
Fig. 3. Binocular rivalry data from Experiment 1. (A) Average dominance duration (shown here pooled over subjects) was not affected by the association strength between the two rivalry processes. Collinear, oblique and orthogonal orientations are grouped together, with separation decreasing from left to right within each group. No systematic variations in dominance duration are apparent despite large variations in the degree of correlation between the two rivalry processes (see Figs. 2A and B). The last set of data points show the remaining six cells from the upper left quadrant of Fig. 1C, arranged in increasing order of orientation difference (relative to the central element). (B) The degree of synchronisation between the two rivalry processes varied markedly despite the constant average dominance times. A randomly drawn 30-s sample (from subject AR) from the two rivalry processes are plotted at two levels of association strength. The top panel shows highly correlated rivalry alternations for the '2.5λ collinear' condition. The bottom panel shows weakly correlated alternations for the '7.5λ orthogonal' condition. The top and bottom panels represent the conditions of maximum and minimum correlation, yet the average of the 'on' phases in each condition are very similar (see A). By contrast, the obvious difference between these conditions is degree of correlation between the two time series, which is far stronger in the top panel ($r = .95$) than in the bottom panel ($r = .07$). (C) The data in (A) suggest that the stochastic alternations of the two rivalry processes remain unaffected by the degree of association between them. Confirming this, the γ distributions of the dominance durations for a Gabor patch in a strongly correlated condition (2.5λ, collinear) and a lowly correlated condition (7.5λ orthogonal) are virtually identical.

mainly when they were very close in spatial location (2.5λ). This may be indicative of the significance of T-junctions, believed to play an important role in image segmentation and depth ordering (Rubin, 2001).

Given the importance of T-junctions, highlighting the presence of adjacent orthogonal elements would clearly be a sensible strategy and it is not surprising that there should be visual processes that renders them salient. This might explain why the association between orthogonal elements was most pronounced for adjacent contours (2.5λ), as these would most resemble potentially important T-junctions (orthogonal associations decreased at a steeper rate beyond 2.5λ than was observed for collinear and oblique orientations: Fig. 2B). There is single cell electrophysiological data demonstrating increased striate firing-rate in response to a central oriented patch embedded in an orthogonally oriented surround (Cavanaugh, Bair, & Movshon, 2002; Jones, Grieve, Wang, & Sillito, 2001; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995) and our findings our also consistent with other psychophysical studies findings indicating that facilitation is not unique to collinear contours (Cass & Spehar, 2005b; Yu et al., 2002). However, whether this is evidence of facilitative contour integration of adjacent orthogonal elements, or merely an example of proximity rendering the orthogonal pair salient is not clear. It could be argued that integration would be the wrong process considering T-junctions are important for image segregation.

The second striking point is that even at quite distant separations, elements tended to associate reasonably strongly. Averaging the data across observers and spatial

frequencies, associations were still significantly greater than zero for the largest separation (10.5λ, oblique orientation: $t7 = 3.73$, $p < .005$) as well as for the largest separation between orthogonal elements (7.5λ, orthogonal orientation: $t7 = 2.15$, $p < .05$). These ranges are slightly longer range than the maximum reported by using the path detection paradigm (Hess et al., 2003), as well as those typically associated with contrast facilitation in lateral masking (2–6λ [(Polat & Sagi, 1993)]), although significant facilitation has been reported at separations up to 12λ (Polat & Sagi, 1994; Tanaka & Sagi, 1998; Williams & Hess, 1998; Woods et al., 2002). Differences between the paradigms probably explain the greater range of facilitation observed here. In our paradigm, the visual field was uniform except for two oriented patches, which were visible for 60 s. It seems probable that the brief exposure durations typically employed in the lateral masking paradigm impose a limit on the spatial range of interactions assuming that the signals must propagate through lateral intrinsic connections, a process that takes considerable time at an estimated speed of ≈ 0.1–$0.3 \, \mathrm{m \, s^{-1}}$ (Bringuier, Chavane, Glaeser, & Fregnac, 1999; Girard, Hupe, & Bullier, 2001; Grinvald, Lieke, Frostig, & Hildesheim, 1994; Nelson & Katz, 1995; Slovin, Arieli, Hildesheim, & Grinvald, 2002; Tucker & Katz, 2003). The brief exposure duration (90 ms) used in lateral masking experiments (Polat & Sagi, 1993) would thus appreciably constrain the range of effective facilitation. Indeed, the minimum exposure duration required to produce facilitation increases between collinear elements increases from 30 ms, for a target-flanker separation of 3λ, to 120 ms for 8λ separations, yielding velocity estimates of lateral

propagation of $\approx$0.1–0.2 ms^{-1} (Cass & Spehar, 2005a). The long, uninterrupted exposure durations employed in the present study may serve to relax the spatial constraints imposed by the comparatively brief exposure durations employed in previous studies.

Finally, we consider the binocular rivalry data. The interesting point that they reveal is that average dominance and suppression periods for a given Gabor in rivalry do not vary as a function of association strength. Regardless of whether one Gabor associates strongly or weakly with a second Gabor, average dominance durations remain approximately constant (Fig. 3A). Rather than the dynamics of the individual rivalry processes varying with association strength, the two rivalry processes instead become synchronised by various amounts, strongly so for adjacent collinear elements, weakly for distant or off-axis elements. Supporting the independence of rivalry dynamics and association strength, the γ distributions of dominance durations for a single Gabor are very similar regardless of whether it is rivalling beside a second Gabor with which it is strongly associated (2.5λ, collinear, upper panel of Fig. 3C) or weakly associated (7.5λ, orthogonal, lower panel of Fig. 3C).

It is interesting that strong facilitative interactions between Gabors engaged in rivalry do not increase dominance duration. These mutual interactions potentially provide a source of activation to the cortical units representing the Gabor patches additional to that elicited by the stimuli in their receptive fields. However, neural adaptation (of neurons signalling the dominant percept) is thought to be the cause of dominance switches (Wilson, 2003), as eventually the representation of the non-dominant percept will become stronger than the dominant one and will at that point become perceptually dominant. Because of this, any additional drive due to lateral interactions would effectively reduce the time constant of neural adaptation, in the same way that an increase of stimulus contrast does. For this reason, the tendency for stronger stimuli to predominate perceptually would be offset by the tendency for strong stimuli to fatigue at a faster rate. This would impose an inevitable limit on how long a percept can be held dominant before a switch occurs, regardless of any additional drive it might receive from strong collinear facilitation.

The independence of rivalry and the association field is important in that it validates the use of rivalry correlations as a measure of association strength. If rivalry dominance durations were influenced by contour association strength, it would be akin to measuring an object with a ruler that becomes distorted by the object it is intended to measure. The independence of rivalry and association strength shows this is not the case and supports our claim that the variations we measure in cross-correlation between the two rivalry processes really do reflect variations in strength of association between two oriented elements. Further support comes the fact that our data overall agree quite closely with those from the lateral masking and path detection paradigms mentioned in the Section 1.

The finding that two rivalry processes can become temporally synchronised indicates that the interactions embodied in the association field concept have a temporal component, in addition to the better-known spatial effects. Only a few studies have examined the temporal dynamics of contour interactions, and most of these have looked at the spread of the associative influence over time and the propagation speed of the associative influence, often using asynchronous stimulus onsets (Cass & Spehar, 2005a; Cass & Spehar, 2005b; Georges, Series, Fregnac, & Lorenceau, 2002). The variations in synchrony that we report point to temporal interactions that operate reciprocally and over a relatively short time frame to align otherwise independent stochastic processes. For adjacent collinear elements, these interactions produce a pattern of oscillatory activity that is almost perfectly phase-locked (collinear elements separated by 2.5λ in Experiment 1 had an average correlation of 0.92). Indeed, it may be the case that the well-known spatial behaviour of the association field is in fact a consequence of temporal interactions and the ability to produce synchronous activity.

3. Experiment 2

Experiment 2 will again map association fields by measuring correlations between local rivalry processes but the effect of contrast (100, 25, and 6%) on association strength is measured rather than the effect of spatial frequency. Contrast is of interest to both aspects of this study because (i) alternation rate in binocular rivalry is known to slow at lower contrasts (Levelt, 1965), and (ii) because weaker direct activation to orientation-selective neurons may result in weaker or longer-latency lateral interactions. In addition, we ran a further condition in which the matrix elements (with the exception of the central element) were rotated by 90° (see Fig. 1D). The main reason for this was that it transforms the horizontal dimension of the matrix from an orthogonal condition to a parallel condition. In testing a parallel condition, we can determine whether it is matched orientations per se that are crucial for strong associations (both parallel and collinear conditions are iso-oriented) or whether orientations must be matched and collinear to produce strong associations strengths (only the collinear condition satisfies this). If the parallel and collinear conditions are equally effective in promoting contour associations, then an account based on grouping by feature identity (i.e., iso-orientation) would more parsimoniously account for the data than association fields.

3.1. Methods

The same observers as in Experiment 1 participated in this experiment. The stimuli, apparatus and procedure were as for Experiment 1 with two exceptions, First, only one spatial frequency was used (4 cpd) and three contrast levels (of Gabors and noise patches) were compared (100, 25, and 6%). We also simplified the matrix of stimulus pairs by

testing only the collinear, oblique and orthogonal dimensions. Since the maps in Fig. 2 appear to be very self-similar, it will be sufficient to measure these three dimensions and fit Gaussians to the data. The amplitude and bandwidth of the fits are convenient parameters that allow easy comparisons with other psychophysical and neurophysiological studies. The second difference with Experiment 1 was that we also included a parallel orientation condition. This was achieved by rotating the matrix elements by 90° (but not the central element: see Fig. 1D), so as to transform the horizontal dimension of the matrix from an orthogonal condition to a parallel condition. This also has the effect of transforming the vertical dimension from collinear to orthogonal, and the oblique dimension from oblique and convex (consistent with smooth closure) to oblique and convex (inconsistent with smooth closure).

3.2. Results

3.2.1. Association field data

Gaussian fits to the data (averaged over observers) are shown in Fig. 4A for three contrast levels (100, 25, and 6%). The plots in Fig. 4A are all roughly congruent and self-similar across contrast levels, just as was observed across the three levels of spatial frequency in Experiment 1. Also as in Experiment 1, the spatial extent of associations depends on relative orientation, with the order of association strength being: collinear > oblique > orthogonal. The main difference between the contrast levels is a tendency for spatial extent

to increase as contrast reduces, as summarised in Fig. 4C (upper panel) where the standard deviation of the best fitting Gaussian for each orientation dimension averaged across observers is shown. Although the main effect of contrast is not significant when averaged over observers as in Fig. 4C, the effect of contrast was significant in analyses of individual data sets. For 4/4 observers, the standard deviation in the collinear condition increased when contrast was reduced from 100 to 6%. The same contrast reduction produced significant increases in standard deviation for oblique and orthogonal dimension in 3/4 observers. The modest effect of contrast is also evident in the similar aspect ratios of the association fields across the three levels of contrast. For 100, 25, and 6% contrast, aspect ratios were respectively: 1.69, 1.93, and 2.02. The increase in aspect ratio with contrast indicates an increased bias towards collinear associations at low contrasts.

Fig. 4B shows the data for the parallel and oblique orientations from the matrix that was rotated by 90° (Fig. 1D). The orthogonal orientation conditions were not tested because they are identical to the orthogonal conditions of the original matrix. The parallel conditions yielded quite strong contour associations, not as strong as observed for collinear conditions, but far stronger than associations observed for orthogonal orientations and roughly equivalent to associations obtained in Experiments 1 and 2 for oblique contours. This is can be seen from the Gaussian fit in Fig. 4B, and also in Fig. 4C where the amplitude of the best-fitting Gaussian is plotted together with data from the
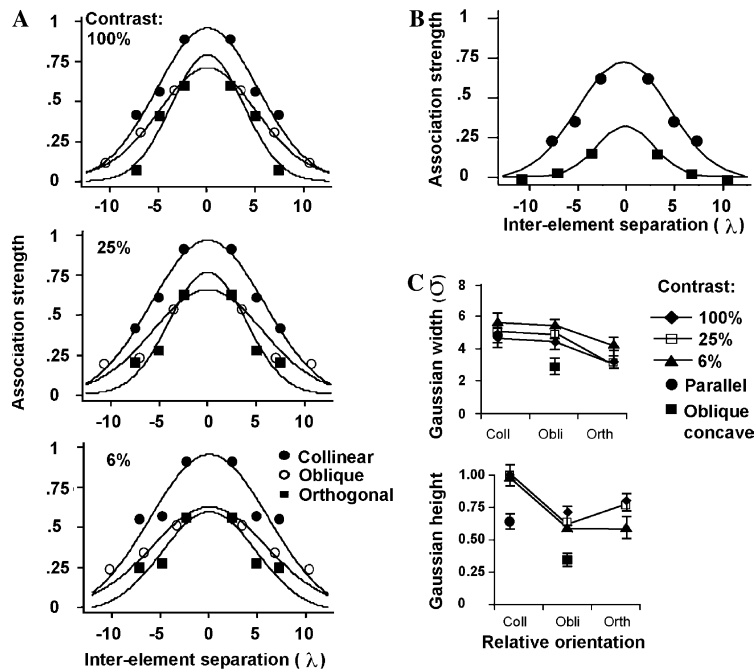

Fig. 4. Association data from Experiment 2. (A) Best-fitting Gaussians fitted to the collinear, oblique and orthogonal dimensions of the matrix (averaged over subjects), shown separately for contrasts of 100, 25, and 6% (from top to bottom). (B) Gaussian fits for the parallel (filled circles) and concave (filled squares) dimensions of the matrix shown Fig. 1D (for which the non-central elements have been rotated by 90°). Contrast was 100%. Note that the oblique dimension is oblique and concave, and therefore not consistent with smooth contour closure. (C) The amplitudes and half-bandwidths at half-height from the best fitting Gaussians shown in (A), as well as those for the parallel condition in (B).

collinear conditions. The aspect ratio for the rotated matrix, given by the standard deviation of the Gaussian fit for parallel weighted by its amplitude divided by the standard deviation of the orthogonal dimension weighted by its amplitude, was close to unity at 1.04, much smaller than the other conditions. Note also that the oblique orientation in the rotated matrix results in a concave pair of contours, where concave in this case means not consistent with smooth contour integration, as opposed to the oblique dimension in the original matrix which produces oblique contours that are convex. While the convex oblique contours result in relatively strong association strength, there is virtually no association strength between oblique concave contours.

The effect of contrast on Gaussian amplitude (Fig. 4A) interacted with relative orientation. While collinear orientations always produced best fitting Gaussian amplitudes of approximately 1.0 (Fig. 4C, lower panel), the amplitudes for

oblique and particularly orthogonal orientations were reduced as contrast was lowered. In 3/4 subjects, the amplitudes of the best-fitting Gaussians for both the oblique and orthogonal dimensions decreased as contrast reduced from 100 to 6%. This effect can be seen in the lower panel of Fig. 4C which shows Gaussian amplitudes averaged across all 4 observers.

3.2.2. Binocular rivalry data

As observed in Experiment 1, there were no systematic changes in rivalry dominance durations (within a given contrast level) across separation or relative orientation. That is, despite dramatic changes in association strength, the average duration of rivalry dominance periods were all very similar, as Fig. 5A shows for three levels of contrast. (This was also true for duration data obtained from the conditions shown in Fig. 4B.) Again, as in Experiment 1, it is variation in the degree of synchrony between the two
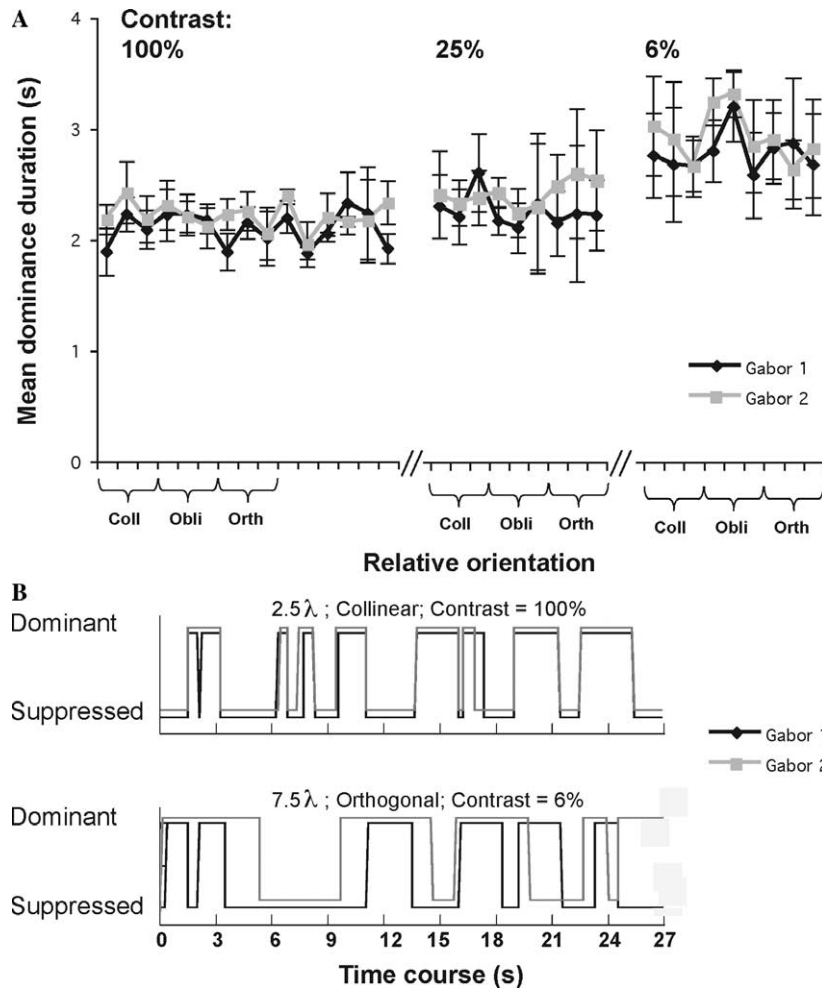

Fig. 5. Binocular rivalry data from Experiment 2. (A) The main difference between the contrast levels is simply a lengthening of average dominance duration (as expected) as contrast reduces. Within each contrast level, average dominance durations (pooled over subjects) were very similar for all separations and relative orientations, despite large variations in the degree of correlation between the two rivalry processes (see Fig. 4A). The data are arranged as described in Fig. 3, grouped by relative orientation and ordered by decreasing separation. (B) A randomly drawn 30-s sample (from subject AR) from a high-contrast, high-correlation condition in the top panel ($r = .93$), and from a low-contrast, low-correlation condition in the bottom panel ($r = .08$). The comparison of the top and bottom panels highlights the longer dominance periods at low contrast as well as the decreased correlation between the time series when separation and relative orientation increase.

rivalry processes that varies systematically with association strength (Fig. 5B). There was however a significant tendency, well established in the binocular rivalry literature (Levelt, 1965), for rivalry alternation rate to slow with decreasing contrast. This is evidenced by significant increases in the average duration of a dominance period (all dominance periods, pooled over all pairings of separation/ orientation) as contrast reduced. For contrasts of 100, 25, and 6%, average dominance durations (with standard errors) were 2.15 s (±.03), 2.33 s (±.08), and 2.84 s (±.08), respectively.

3.3. Discussion

In analyses of individual subject's data, both Gaussian amplitude and width were significantly influenced by contrast changes. The effect of reducing contrast can be summarised as a lowering of the strength of association (except for collinear orientations) and an increasing of the spatial range of association. The effects, though, were relatively modest, with these effects not being significant in an analysis where data was pooled over observers (where inter-subject variability was sufficient to obscure the effects). Explorations of the effect of contrast in other paradigms have also concluded that contrast has limited effects (Hess et al., 2003; Polat & Sagi, 1993).

One reason for the lack of a strong effect of contrast may be that contrast was not reduced enough to reveal them. It has been shown that there are important changes in the facilitation/inhibition patterns of V1 units which begin to emerge once contrast drops to around 5% or so (Sceniak, Ringach, Hawken, & Shapley, 1999). In the paradigm used here, very low contrasts are not viable because of Troxler's fading, the name given to the tendency for low contrast targets to fade with prolonged fixation, especially when peripherally imaged. The targets in this experiment were located on a virtual circle with a radius of 6λ around the point of fixation. A condition at 3% contrast was piloted but with the long period of fixation used in these experiments (60 s) Troxler's fading was frequently observed and this conditions therefore had to be abandoned. Thus, the lowest contrast level of 6% used here may not have been low enough to produce strong contrast effects. However, the contrast effect we did observe (increased spatial extent of association as contrast was lowered), however modest, was at least consistent with claims (Sceniak et al., 1999) that the facilitatory centre of a neuron's receptive field expands as contrast is lowered and colonises the surrounding inhibitory region. Less inhibition and increased extent of facilitation square with contrast producing an increased spatial range of association.

Finally, the data shown in Fig. 4B are interesting. Data from the oblique conditions did not replicate the findings from Experiment 1. The reason for this is probably that the obliques in Experiment 1 are convex and therefore 'relatable' (Kellman & Shipley, 1991), meaning that they are consistent with smooth closure, whereas the obliques in the

rotated matrix of Experiment 2 have a convex relationship and are not consistent with smooth closure. Another important point from the data in Fig. 4B is that the parallel conditions were much less effective at eliciting contour associations than were collinear orientations. Gaussian amplitude in the parallel condition was significantly lower than that in the collinear condition for the same spatial frequency (4 cpd) and contrast (100%). This is important because it demonstrates that it is not iso-orientation per se that determines association strength, as both parallel and collinear conditions are iso-oriented, but rather it is collinearity that is necessary to allow strong collinear facilitation.

4. Experiment 3

In Experiments 1 and 2, the stimuli were presented always within one visual hemifield. Thus the two Gabor elements projected to the same hemisphere and presumably activated columns of orientation-selective neurons in V1 that were located in relatively nearby locations (Bonhoeffer & Grinvald, 1991; Chisum et al., 2003). The nature of lateral intrinsic connections between neighbouring orientation-selective units in V1 is well established and are likely to play a vital role in the associations we report in Experiments 1 and 2. In Experiment 3, however, we will present the Gabor elements on opposite sides of the vertical midline, so that each stimulus will activate orientation columns in separate hemispheres, and then re-measure the association field.

4.1. Methods

Methodology was virtually identical to that of Experiment 1. The only important difference was that the virtual circle on which the stimuli were located was divided vertically into two helves and shifted laterally by half a degree either side of the vertical midline to ensure that the stimuli would activate separate cortical hemispheres and not central regions of foveal overlap. Although stimuli were located on a horizontally defined semicircle in this experiment (compared with the vertically defined semicircle used in Experiments 1 and 2), the randomisation of location around the circle together with the range of orientations in the matrix meant that in both experiments a full range of orientations was present over trials. The only constraint in this experiment was that the elements' locations had to span the vertical midline, to be sure to activate separate cortical hemispheres. Only one spatial frequency was tested (4 cpd), with two levels of contrast for the Gabors and noise patches compared (100 and 10%).

4.2. Results

4.2.1. Association field data

Gaussian fits to the interhemispheric data are shown in Fig. 6A for two contrast levels (averaged over 4 observers). Overall, the pattern of results is rather similar to those
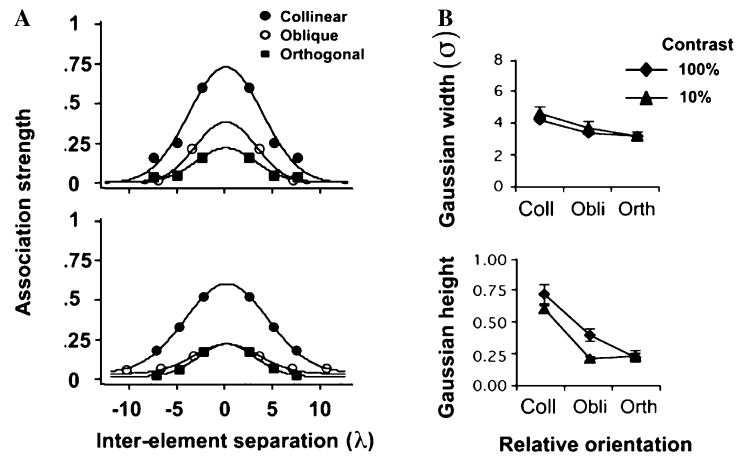
Fig. 6. Association data from Experiment 3 (interhemispheric presentation). (A) Best-fitting Gaussians fitted to the collinear, oblique and orthogonal dimensions of cross-correlation data (averaged over subjects). Top panel shows 100% contrast, bottom panel shows 10% contrast. (B) The amplitudes and half-bandwidths at half-height from the best fitting Gaussians to the data shown in (A). The main difference from the within hemisphere presentation is that association strengths are reduced overall and are mainly evident for collinear orientations (see Figs. 2 and 4).

obtained within hemispheres in Experiments 1 and 2, although there are two quantitative differences: amplitudes (strength of association) are significantly reduced in the inter-hemispheric data, as are widths (extent of association). Fig. 6B plots amplitude and width for the interhemispheric data, and also replots the 4 cpd within-hemisphere data from Experiment 1 (4 cpd, 100% contrast) for comparison. In the upper panel of Fig. 6B, the comparison with the within hemisphere data highlights the reduced extent of association strength in the interhemispheric condition. The interhemispheric data did not differ significantly in extent across the two contrast levels, again indicating that the role of contrast in contour associations is slight. However, the average extent of association across both contrast levels was significantly less than the spatial extent shown for the within hemisphere condition replotted from Experiment 1 ($t36 = 5.97$; $p < .001$).

The strength of association was also weaker for the interhemisphere condition. The lower panel of Fig. 6B shows the Gaussian amplitudes from the fits in Fig. 6A, together with amplitudes (averaged over contrast) taken from Fig. 4B (Experiment 2) for comparison. Relative to the within hemisphere condition, where association strengths were all approximately 1.0 for the collinear condition, strength of association is clearly reduced in the interhemisphere condition, peaking at around 0.75 for collinear orientations, and much weaker for oblique and orthogonal orientations. The average amplitude of the within hemisphere data from Experiment 2 is significantly greater than the average amplitude for the interhemisphere data ($t58 = 16.75$; $p < .0001$). In addition, for the interhemisphere data alone, the collinear amplitude was significantly greater than the oblique ($t14 = 6.53$, $p < .001$) and the main effect of contrast was significant ($t22 = 2.20$, $p < .025$).

4.2.2. Binocular rivalry data

As observed in Experiments 1 and 2, the average duration of rivalry dominance phases exhibit no dependence on association strength. Average dominance durations are very similar for all separation/orientation pairings (Fig. 7A), with the degree of synchrony between the two rivalry processes being responsible for the variations in association strength (Fig. 7B). However, dominance durations in the interhemisphere conditions are shorter than for the within hemisphere condition. At 100% contrast, the average duration (and standard error) between hemispheres was 1.46 s ($\pm.03$) compared with 2.15 s ($\pm.03$) for within hemispheres. Also, the tendency for dominance duration to lengthen as contrast is lowered is more pronounced for between hemisphere rivalry, with a shift from 100 to 10% contrast lengthening average dominance from 1.46 to 2.70 s (85% increase in duration), while the shift from 100 to 6% contrast only lengthened dominance from 2.15 to 2.84 s in the within hemisphere condition (32% increase in duration).

4.3. Discussion

Experiment 3 was designed to shed light on the nature of contour associations between hemispheres. The two significant aspects of the data are that interhemispheric associations are weaker overall than within hemisphere associations (Fig. 6B, upper panel), and are shorter in spatial extent (Fig. 6B, lower panel), particularly when between non-collinear elements. The finding of weaker associations agrees with a more limited interhemispheric investigation carried out by Alais and Blake (1999), although the fact that collinear and adjacent Gabors still underwent strongly correlated rivalry alternations (approximately 0.7 when contrast was high) seems to imply that interhemispheric connections mediated by callosal fibres maintain a reasonable degree of strength and accuracy in targeting columns of similar orientation preference despite being of greater physical length than within hemisphere connections. Indeed, the data suggest that interhemispheric contour
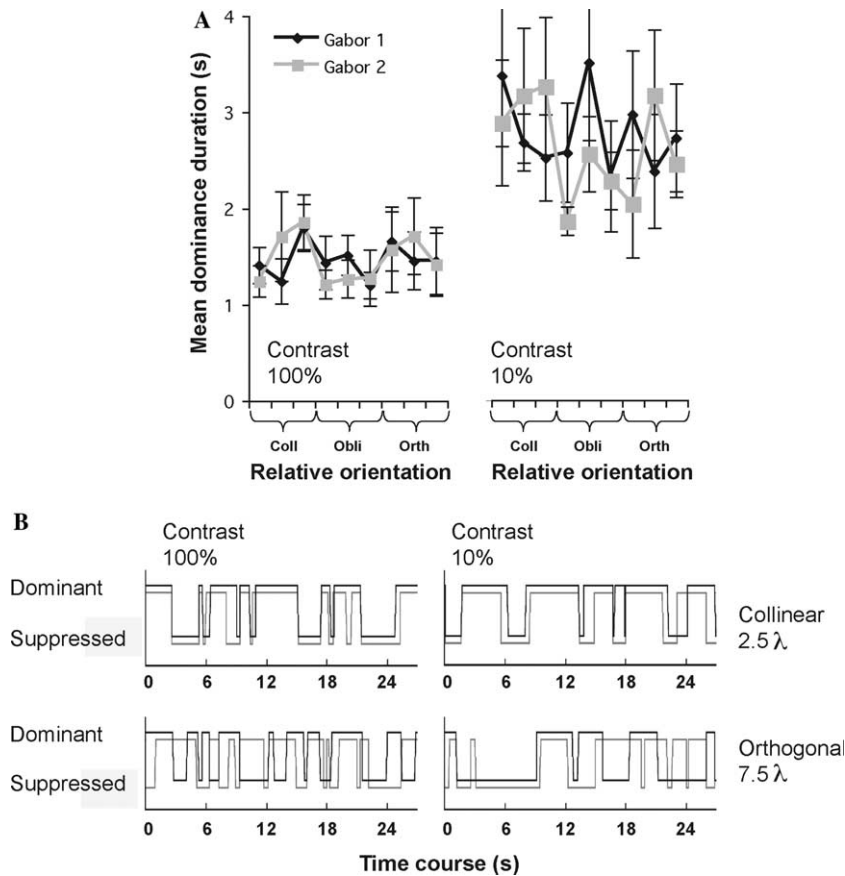
Fig. 7. Binocular rivalry data from Experiment 3 (interhemispheric data). (A) As for within hemisphere presentation, average dominance durations for all separations and relative orientations were very similar despite large variations in the degree of correlation with the second rivalry process. However, compared with the within hemisphere data from Experiment 2 (see Fig. 5), interhemispheric rivalry exhibited shorter dominance durations at 100% contrast and a stronger dominance lengthening effect as contrast reduced. Data arranged as in Figs. 3 and 5. (B) As for within hemisphere presentation, it was the degree of synchronisation between the rivalry processes that differed between the conditions, not the average dominance durations. 30-s samples drawn from the time series of the two rivalry processes are plotted at two levels of association strength (top row vs. bottom row) and at two levels of contrast (left pair vs. right pair).

interactions are primarily between collinear units, as the aspect ratios of the interhemispheric association fields are much larger than those for within hemisphere associations. For 100% contrast, the aspect ratio was 4.57, and for 10% contrast, the ratio was 4.00. Ratios greater than 1 indicate a bias towards collinear associations, and these interhemispheric values are more than twice the size of within hemisphere aspect ratio (which averaged just 1.82 in Experiments 1 and 2).

The main reason for the high aspect ratio is that Gaussian amplitudes for oblique and orthogonal orientations are much lower in the interhemispheric condition than in the within hemisphere condition (since amplitude is used to weight the ratio Gaussian standard deviations in the aspect ratio calculation—see Results, Experiment 1). However, the fact that associations are biased towards collinear may instead be due to another explanation, that of higher-level feedback. Since collinear Gabors are most easily grouped into a perceptual whole, feedback may favour collinearity over other relative orientations. If there were no systematic callosal connections to facilitate contour integration, then feedback would be the only mechanism and a stronger ten-

dency for collinear facilitation would be evident. If a role for feedback is acknowledged, then it would also be involved in the within-hemisphere condition, although in this case it would presumably operate in addition to the well-documented effect of intrinsic lateral interactions (i.e., the association field) which would account for the broadening of the association tuning to non-collinear relative orientations.

Overall, it is clear that contour associations and association fields can be demonstrated for interhemispherically presented Gabors. As with the within hemisphere associations reported in Experiment 2, contrast does not greatly affect interhemispheric associations. On one account, interhemispheric associations would be consistent with the argument that similar organizations should exist for inter- and intra-hemispheric connections as both subserve similar functions (Innocenti, 1986; Schmidt, Goebel, Lowel, & Singer, 1997). Alternatively, interhemispheric association fields might reflect feedback from higher areas that group collinear elements into larger wholes. One way to test between these alternatives would be to study synchrony in the very early part of the display (the first hundred

milliseconds or so). Feedback-mediated synchrony should take longer to appear than synchrony mediated by lateral connections, since signals propagate through lateral connections much faster than via feedback. The present paradigm, unfortunately, is not well suited to this, as the variance of observers' reaction times as they press keys to monitor their rivalry alternations would probably obscure the small synchrony effects—even with many hundreds of trials. A brief paradigm, however, such as flash suppression (Alais & Blake, 2005), might permit a distinction between these accounts.

5. Summary and conclusions

The aim of the present paper was to describe the associative links between local oriented elements by measuring cross-correlations between two binocular rivalry processes. The motive for employing a binocular rivalry paradigm was that it provided a means for studying contour interactions at high contrast (rather than at threshold, as in Polat and Sagi's lateral masking method) and without the masking effect of surrounding noise elements (as in the Hess group's pathfinder paradigm). By measuring the degree of cross-correlation between the two rivalry processes as a function of element separation and relative orientation, a topography of lateral interactions was obtained. These 'association field' maps agree in important qualitative ways with the findings of other approaches in that: (i) association strength was strongest for collinear elements and weakened with spatial separation, (ii) the maps were largely self-similar across spatial frequency, and (iii) the maps did not show a particular dependence on contrast. Quantitatively, a couple of differences were notable between our results and those obtained using other paradigms. First, the spatial extent of contour associations was greater than is typically implicated in other methods. Along the collinear dimension, correlations were still well above zero at separations of 7.5λ. Second, there was no relative orientation at which significant associations were not possible, although associations between orthogonal elements were clearly shorter in spatial range than between collinear elements, perhaps indicative of a tuning for T-junctions.

One very interesting finding is that the dynamics of the individual rivalry processes are completely independent of the strength of association between them (Figs. 3 and 5). Regardless of whether two rivalry processes are very highly correlated (as in the near-perfect correlations observed for collinear Gabors separated by 2.5λ) or not (orthogonal Gabors separated by 7.5λ), the average duration of dominance of each Gabor (and hence the rivalry alteration rate) is roughly invariant. This gives us confidence that the rivalry processes do not impinge upon the contour association strengths we seek to measure. Clearly, if the rivalry process were to vary with or interact with association strength, teasing apart the rivalry and association field effects would be a complicated task. On the contrary, the degree of synchrony between these two local stochastic processes reveals the pattern of contour interactions between the two Gabor patches. Synchrony between two processes would clearly require a conduit for communication, and the most likely candidate for this role is the network of lateral intrinsic connections in V1. Since association fields are meant to integrate contour segments into global contours, a synching-in process would make sense as it would allow a collection of contour elements to be represented as a global contour through oscillatory binding (Singer & Gray, 1995).

In Experiment 3, we were surprised to see the relatively high degree of association between two rivalry processes activating different cerebral hemispheres. If the synchronisation of two stochastic (rivalry) processes requires a conduit to enable communication, then the conduit between hemispheres can only be the fibres of the corpus callosum. Judging from the quite strong rivalry correlations seen in our interhemispheric data, callosal fibres must be quite specifically targeted to corresponding locations in the contralateral hemisphere and also well targeted to matching stimulus attributes within those locations, especially collinear orientations. Indeed, a strong bias to collinear orientations was the main difference between the interhemispheric and the within hemisphere data, as revealed by the aspect ratios in Experiment 3 being more than twice as large as those in Experiments 1 and 2. Apart from this, the other distinction between the interhemisphere and the within hemisphere data is that the spatial extent and amplitude of contour interactions are less when the stimuli are presented to separate hemispheres. This difference could indicate that callosal connections are weaker and/or less distributed across relative orientation than connections within hemispheres but otherwise broadly similar (preserving the idea of similar functional connectivity within and between hemispheres). Alternatively, it could be that feedback from higher-level areas that group based on contour collinearity could mediate these effects.

Finally, it is noteworthy that no combination of separation and relative orientation was sufficient to reduce the correlation between the two rivalrous processes to zero (see Section 3.3), not even orthogonal elements separated by 7.5λ. Several points might explain this. First, if orthogonal facilitatory interactions fail to map onto the known functional connectivity of V1, other mechanisms could be considered. One potential candidate is area V2 whose pattern of horizontal connectivity has been found to link cells of orthogonal orientation preference (Matsubara, Cynader, & Swindale, 1987). Second, given that our stimuli were presented for 60-s periods, it is possible that very weak long-range connections became significant because the extended stimulus duration provided time for a resonance between two cell populations time to build up (but would be ineffective in short-duration paradigms). A final possibility is that two bistable stimuli simultaneously present in the visual field might tend to oscillate together regardless of contour associations so that there is always a significant baseline of correlated oscillatory behaviour.

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