



A transition between eye and object rivalry determined by stimulus coherence

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Abstract

Two orthogonal patterns presented to the two eyes, respectively, are perceived as alternating in time, a phenomenon often assumed to reflect competition between neuronal activities corresponding to the two eyes, presumably in the primary visual cortex. Recent evidence supports a competition between neuronal activities corresponding to the two patterns (objects) at some higher cortical processing stage after inputs from the two eyes have converged. Here, using textures made of Gabor signals, we present psychophysical data showing that the level of visual processing at which competition takes place and is resolved, is determined by the degree of stimulus coherence. Moreover, depending on stimulus parameters, competition may occur at several levels of processing at the same time. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

For more than a century binocular rivalry has held an important place in discussions of perception and attention because it was considered to reflect an internal selection process that affected visual awareness in a critical way (see Walker (1978) for review). Yet, despite an intensive research effort, recently motivated by a renewal of the search for the neural basis of consciousness (Crick, 1994), there is still a debate on the fundamental question: at what level of visual processing are the two competing retinal inputs resolved into a single (although alternating) coherent percept? That is, what gains perceptual dominance in binocular rivalry — Is it the input to one or other eye or the perceived patterns (visual objects)?

The eye competition view holds that binocular rivalry is resolved at a monocular level, possibly via reciprocal inhibition between pools of V1 monocular cells (Lehky, 1988; Blake, 1989; Mueller, 1990). This view is sup-

ported by behavioral studies that show that suppression during rivalry is non-selective over a broad range of stimuli, so that any stimulus changes presented to the suppressed eye go unnoticed until seconds later (Blake, & Fox, 1974; Blake, Lokey, & Norman, 1998). Moreover, switching stimuli between the two eyes immediately after one eye gains dominance, switches the perceived pattern while the same eye remains dominant (Blake, Westendorf, & Overton, 1980), indicating non-selective competition between two monocular sources. A recent fMRI study (Polonsky, Blake, Braun, & Heeger, 2000) provides further support to the sensory competition hypothesis, by showing a correlation between activity changes in V1 and the observed perceptual alternations. Nevertheless, other recent findings from psychophysical and physiological studies are inconsistent with the eye competition view and, to the contrary, suggest that coherent interpretations of images, rather than monocular information sources, compete for perceptual dominance (Sengpiel, 1997; Logothetis, 1998). Physiological studies show that the activity of binocular but not monocular cells correlates with perceptual alternations induced by rivalry with increasing reliability as one ascends through the ventral visual pathway (18% of cells recorded in V1/V2, 38% in

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V4, 90% in IT) (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997). Logothetis, Leopold and Sheinberg (1996) have found that a pair of orthogonal gratings induced orientation rivalry even when swapped between the two eyes at the rate of 3 Hz. These results suggest that the oriented patterns rather than the eye to which they were presented, dominated perception, hence, pattern-rivalry. This view is also consistent with the more traditionally held notion of central selective processes involved in binocular rivalry (Breese, 1909; Walker, 1978), with recent evidence for the effect of attention in rivalry (Ooi & He, 1999), with recent evidence for inter-hemispheric switching coupled with rivalrous perceptual alternations (Miller, Liu, Ngo, Hooper, Reik, Carson, & Pettigrew, 2000), with evidence for interocular grouping in rivalry (Diaz-Caneja, 1928; Wade, 1973; Kovács, Papathomas, Yang, & Feher, 1996) and with the observed similarity between the properties of binocular and monocular rivalry (where orthogonal patterns viewed monocularly engage in perceptual alternations) (Campbell, Glinsky, Howel, Riggs, & Atkinson, 1973b; Andrews and Purves, 1997). One is left, therefore, with conflicting results. On the one hand, pattern rather than eye-rivalry and on the other hand, clear indication for non-selective eye suppression (Blake & Fox, 1974; Blake et al., 1980). Lee and Blake (1999) argued that the apparent contradiction is due to a comparison between different types of rivalry. They found that pattern-rivalry induced by rapid swapping occurs only in a very limited range of spatial-frequency and swapping rate, suggesting that it is a different and special case of perceptual ambiguity resolved by perceptual alternations.

Here we examine the possibility that the degree of global coherence of stimuli presented to the two eyes may determine the involvement of eye- and pattern-specific mechanisms, or more generally, the level of processing at which rivalry occurs. Global coherence, corresponding to texture uniformity and contour smoothness, was found to have an important role in short duration rivalry (Bonnef & Sagi, 1999), pointing to excitatory and inhibitory processes in primary visual cortex underlying region grouping and segregation, respectively. At this processing stage, nonuniform stimuli (e.g. textures made of random orientation patches) produce highly salient activity compared with large uniform stimuli, that are probably made available as objects for higher levels of processing (Bonnef & Sagi, 1998, 1999). We observed that when similar stimuli were tested using the swapping paradigm of Logothetis et al. with a pair of locally orthogonal textures composed of Gabor patches replacing the orthogonal gratings, largely spaced or randomly oriented patches induced eye-rivalry, rather than pattern-rivalry (Bonnef et al., 1998, Society of Neuroscience Abstract). Thus, instead of a stable percept of one pattern slowly and

irregularly alternating with the other pattern, the two patterns were perceived as switching regularly three times a second, with each Gabor patch locally rotating, indicating the dominance of input from one eye (Fig. 1).

We studied this phenomenon systematically, by manipulating three stimulus dimensions: orientation uniformity, proximity and size. Stimuli were viewed dichoptically and always consisted of a pair of stimuli containing locally orthogonal Gabor patches (see Fig. 2). These stimulus dimensions were tested in three different experimental conditions: ‘ocularity’, in which subjects had to report the nature and stability of the percept when presented with fast between-eye swapping stimuli; ‘rivalry speed’, in which the rate of alternations between two competing stimuli (as in classical rivalry with no between-eye swapping) was measured as a function of stimulus coherence and ‘contrast invariance’, in which the stimulus-contrast dependency of binocular rivalry was measured. Whereas, the first condition directly addresses the issue of eye versus pattern-rivalry, the last two conditions provide evidence on the integration processes involved in the disambiguation of rivalry.

2. Methods

2.1. Stimuli

Observers viewed a pair of orthogonally oriented configurations of Gabor patches, with global rightward tilt (45°) to one eye and leftward (-45°) to the other, and with local orthogonality of corresponding patches (Fig. 2 top). The spatial-frequency of the Gabor signals was 4.2 cycles per degree in all experiments. Testing the effect of orientation jitter and spacing was performed using an array of 5×5 Gabor patches ($\sigma = \lambda = 0.24^\circ$, σ , the Gaussian envelope parameter and λ , the wavelength, from $3^\circ \times 3^\circ$ to $5^\circ \times 5^\circ$ in size). To test orientation jitter (Fig. 2 top left), spacing was fixed at 2λ and local Gabor orientation was selected at random in the range of $r/2..r$, $-r/2..-r^\circ$ (in addition to the global tilt), with r (randomization range) varying between blocks from 0 (collinear) to 40 (highly randomized, but the global tilt still easily identified) in 10° steps. To test the effect of spacing (Fig. 2 top middle), orientation was kept uniform (collinear) and inter-element spacing was varied between 2λ and 4λ in steps of 0.5λ . To test the effect of stimulus size (Fig. 2 top right), a single Gabor patch ($\lambda = 0.24^\circ$) was presented to each eye, with envelope varied between blocks from $\sigma = 0.24^\circ$ to $\sigma = 0.72^\circ$ in steps of 0.12° . To test the level of eye-dominance relative to stimulus-dominance during rivalry, we applied the swapping paradigm of Leopold and Logothetis (1996). The above stimuli were

flickered synchronously in each eye at 15 Hz (flashes of 33.33 ms durations (two frames) that were separated by intervals of 33.33 ms) and swapped every 333 ms between the eyes. Stimulus contrast (defined by the amplitude of the generating Gabor signal relative to mean luminance) was fixed at 0.7, except for testing rivalry speed, in which case contrast was varied between blocks in the range of 0.25 to 0.7 (both eyes), with a random order of blocks. Stimulus contrast for testing the effect of relative contrast was varied in a similar way, except that contrast level to one eye was kept constant at 0.7. In all stimulus conditions, a pattern of transparent black random-dots (dot probability of 3%) was added to the Gabor configuration and displayed continuously (even when the configuration was flickered) to aid proper convergence.

2.2. Apparatus

Stimuli were displayed as gray-level modulation on a 20-inch Sony GDM2000-TC color monitor, located 1.5 m from the eyes of the observer, using a Silicon Graphics Crimson/Reality Engine system. The video format was 120 Hz interlaced with 1280×450 pixels for each eye occupying a $19 \times 15^\circ$ area. Stimuli were viewed

with CrystalEyes E-1 stereo glasses with optic shutters that alternate at 120 Hz synchronized with the monitor. The effective display luminance when viewed with the stereo glasses was 7 cd/m^2 . The cross-talk between eyes (due to the screen's phosphor afterglow and the dynamic range of the shutters) was $\approx 7\%$ (see Bonnef and Sagi (1999) for more details on stereo apparatus). An 8-bit RGB mode was used and Gamma correction applied to produce a linear behavior of the displayed luminance.

2.3. Experimental procedures

Sessions consisted of three sets of blocks, each set testing one stimulus condition (orientation jitter, spacing or size) and one paradigm (ocularity, rivalry speed or relative-contrast effect) and lasted for ≈ 60 min (three sets of 15 blocks, each with one trial of 1 min, with short breaks between sets). Block order was randomized between sessions, except that contrast was kept constant within a set when measuring rivalry speed and only varied between sets. Observers repeated each experimental condition three times. The observers viewed the stimuli for periods of 60 s (blocks) and reported the dominant stimulus by depressing the left/

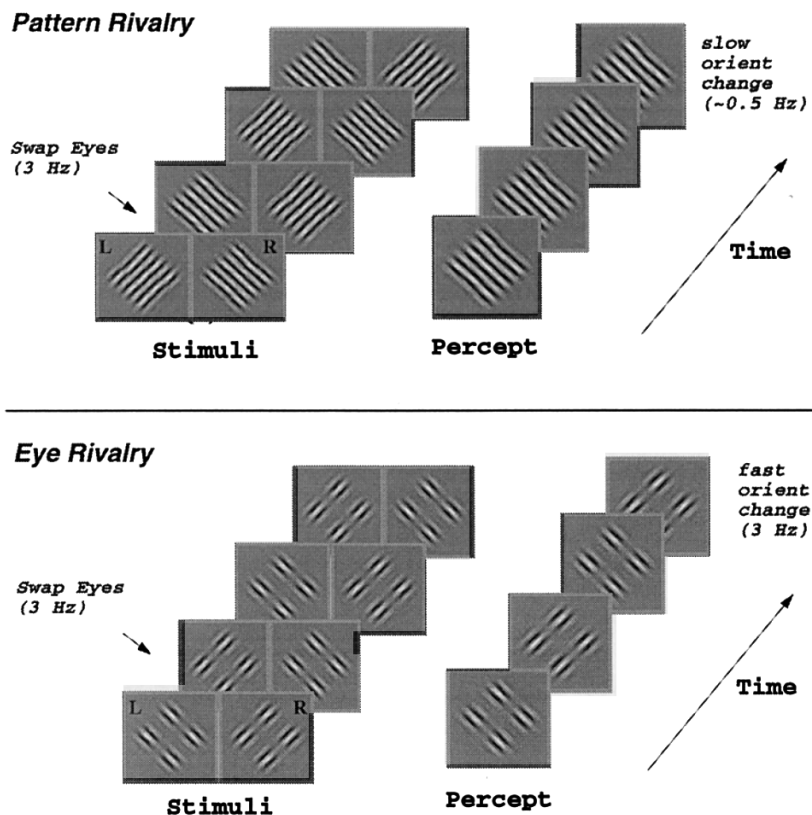


Fig. 1. Stimulus pairs tested dichoptically and swapped between the eyes at 3 Hz. Top, a densely spaced uniform Gabor texture which induces alternating percept of either one or the other orientation, each appearing stable for several seconds (pattern-rivalry). Bottom, a largely spaced Gabor texture, which is perceived as if each patch (local element) is rotating regularly, following the 3 Hz eye swapping rate (eye-rivalry with the input to one eye dominating).

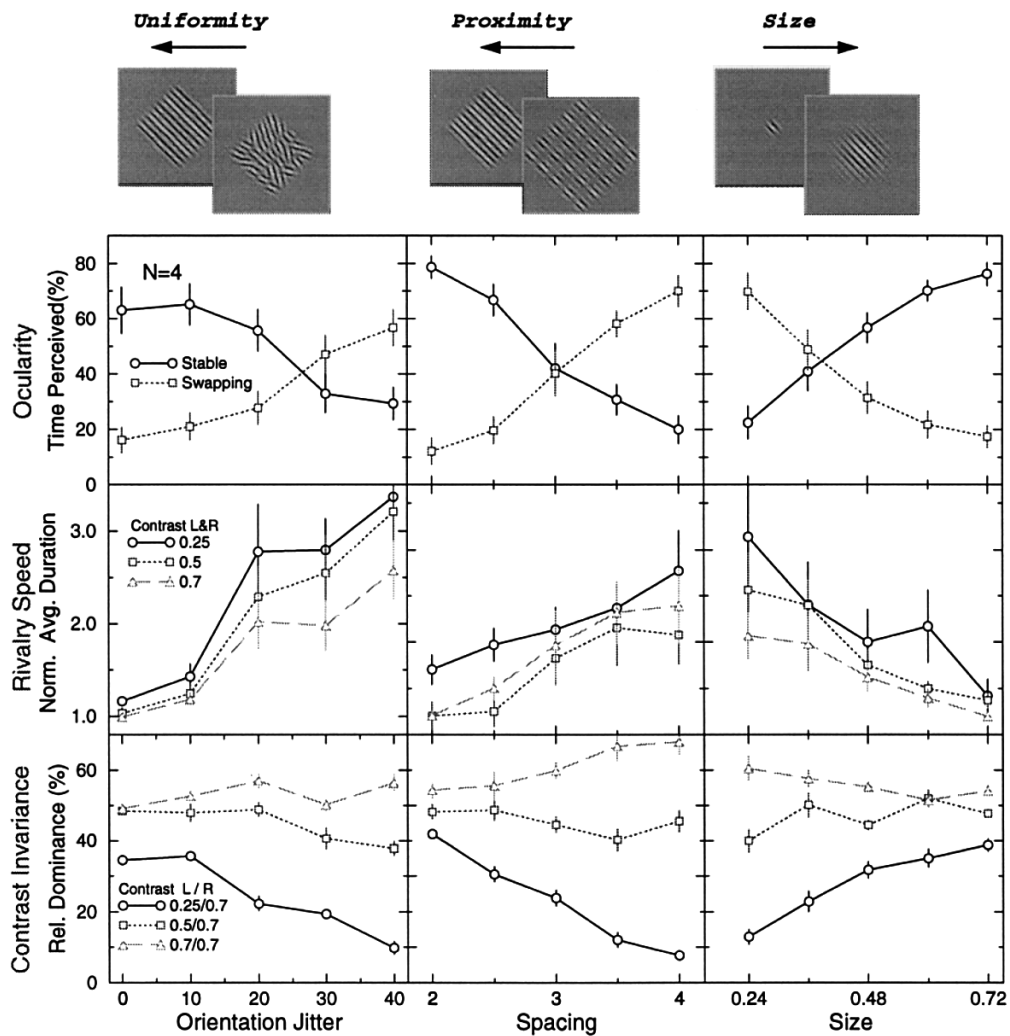


Fig. 2. The effect of global coherence (columns) on different aspects of binocular rivalry (rows). Spatial configuration (global coherence) was manipulated in three dimensions: Orientation uniformity (left, in orientation jitter degrees range (\pm)), Spacing (middle column, in wave-length units) and size (right, in pixels defining the Gabor's σ parameter). Three aspects of binocular rivalry were measured: ocularity (top row) was measured using the swapping paradigm of Logothetis et al. (1996). The graphs (top row) show the percentage of time in which the stimuli were perceived 'stable' (solid line) or 'swapping' (dotted line), averaged across four observers. Note that rivalry becomes more ocular (longer 'swapping' periods and shorter 'stable' periods) with increasing orientation jitter and spacing and with decreasing size. Rivalry speed (middle row) was measured by recording dominance phases during 1 min periods of rivalry (no swapping). The graphs show the normalized mean dominance durations (four observers) for three contrast levels. Note that rivalry slows-down with orientation-jitter, increased spacing and decreasing size. Contrast invariance was tested by measuring the relative dominance of one eye (relative accumulated dominance period) whose contrast was varied (0.25, 0.5, 0.7 in separate plots) keeping the contrast of the other eye fixed (0.7). Note that the contrast difference between the eyes has a stronger effect with increasing orientation jitter and spacing and with decreasing size as indicated by the slope of the relative-dominance curves. Overall, increased global coherence makes binocular rivalry less ocular (stimulus rather than eye-rivalry), faster in alternation speed and more invariant to contrast differences between the eyes.

right mouse buttons for the perceived leftward/rightward tilt. When incomplete dominance was perceived (e.g. local dominance to different directions), the subject was instructed not to press any button. In testing eye-dominance relative to stimulus-dominance (using the swapping paradigm), the observers were instructed to depress a third button (middle mouse button) whenever rapid regular changes were perceived.

Six observers, including two of the authors (YB, AK), with normal or corrected vision and normal

stereopsis, participated in the experiments. Four observers were naive as to the purpose of the experiments and were paid for participation. Four observers participated in each experimental condition.

3. Results

The results are summarized in Fig. 2, with the columns representing the three stimulus dimensions and the rows representing different experimental conditions.

3.1. Ocularity

In the ‘ocularity’ condition, observers had to depress and hold one of two buttons when a stable orientation was observed (left or right tilt), a third button when a fast regular change of orientation was observed and no button in any other case (e.g. when the display was perceived as partially tilted left or partially tilted right (see Section 2). In this way, observers were not biased to impose a stable pattern interpretation, as in the Logothetis et al. (1996) study and were not limited to short 10 s epochs, as in the Lee and Blake (1999) study. Results are shown in Fig. 2 top row. Two curves were plotted for each stimulus dimension, one (solid line) for the relative times of perceiving stable percepts (in any orientation) and the other (dotted line) for perceiving a fast regular change in orientation: perception of the ‘swapping’. The relative duration for perceiving a stable, globally oriented percept, decreased monotonically from 60–80% of presentation time for a dense uniform texture or a single large Gabor patch ($\sigma = 3\lambda$) to 20–30% for jittered orientation ($\pm 40^\circ$), larger (4λ) spacing or a single small patch ($\sigma = \lambda$). This reduction was not due to non-exclusive visibility or split dominance (different orientations at different areas), but rather to an increase in the duration of perceiving fast regular changes (swapping), as seen by the complementary ‘swapping’ curve moving down from 20–30 to 60–80%. Increasing stimulus size, which we found to decrease eye-rivalry is also known to decrease exclusive visibility in rivalry (Breese, 1909; Blake, O’Shea, & Mueller, 1992; O’Shea, Sims, & Govan, 1997), suggesting a distinction between local ocular competition and the more global pattern-rivalry. Note that inaccurate eye convergence could potentially cause patches from different eyes not to overlap (for large spacings) and thereby enhance eye-rivalry. However, the use of a transparent random dot pattern as a fixation cue minimized this effect. Observers’ attention could also have affected the results, as many observers noted that swapping pattern was perceived locally whenever they fo-

cused (attended) a small area. Two observers could not see the stable percept at all, unless color was applied to each pattern (see Logothetis et al. (1996) for a similar observation).

3.2. Coexistence

If one accepts that coherence across a specific stimulus dimension determines the level at which rivalry is resolved, one should consider the possibility that by manipulating two stimulus dimensions, pattern and eye-rivalry may come to co-exist. Although other types of coexistence in binocular vision have been previously demonstrated (e.g. Mayhew & Frisby, 1976; Carney, Shalden, & Switkes, 1987), the isolation of eye- and object-specific mechanisms and their possible coexistence were never tested. To test this, we assigned a different color to each eye, thus only patterns but not colors were swapped between eyes and the color assigned to each orientation changed with every eye swap. Under these conditions, pattern-rivalry would presumably be perceived as stable orientation with fast color changes and eye-rivalry as fast orientation changes with slow color alternations. The results, however, were quite different — most of the time, none of the above percepts were reported. Instead, long periods of a stable color and orientation were perceived, which imply eye or color rivalry independent of orientation rivalry (see Wolfe (1986) for review of earlier observations of this sort and Carney et al. (1987) for independent color rivalry and motion perception). Nevertheless, the effects of global coherency manipulations were similar, with an increase of eye-rivalry relative to pattern-rivalry when larger spacing or orientation jittering of the texture elements were introduced. In a second experiment, we used a pattern that was composed of a dense uniform Gabor-texture (background) and four largely spaced, oblique patches (foreground). An example of such a stimulus is shown in Fig. 3. Two such locally orthogonal patterns induced pattern-rivalry of the background and eye-rivalry of the

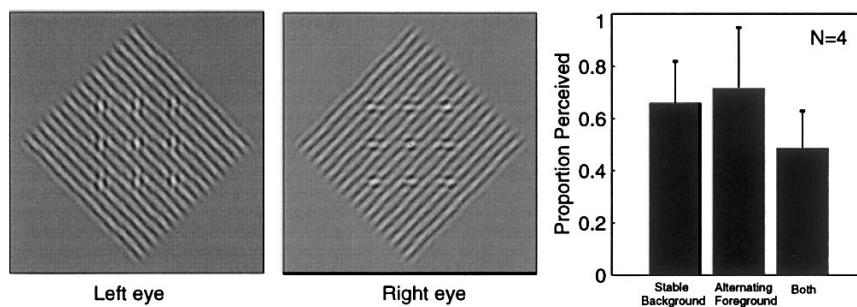


Fig. 3. Coexistence of pattern- and eye-rivalry. Left—stimuli made of a background of dense uniform textures and a foreground of six largely spaced patches. The observers had to monitor the orientation of the background (if stabilized despite the fast eye swapping) and depress a third button when the foreground patches were perceived as undergoing fast regular alternations. Right—proportion perceived rates for stable background (either orientations), alternating foreground and both simultaneously, for four observers.

oblique patches. Observers reported simultaneously on the background orientation (by pressing either the left or right mouse buttons), and if fast regular alternations of the isolated patches were perceived, by pressing the middle button. For the four observers tested, a stable background was perceived during $61 \pm 5\%$ of the viewing time and a fast regular swapping of the foreground patches for $67 \pm 7\%$ of the viewing time (values denote average and S.E.). This shows that eye- and pattern-rivalry can coexist at the same time, using stimuli of identical spatial-frequency and different orientation. (See Mayhew & Frisby (1976) for a different type of coexistence in binocular vision, that of fusion and rivalry in different spatial-frequency channels).

3.3. Rivalry speed

The rate of alternations (rivalry speed) of the two competing percepts was found to be dependent on the coherence of the stimuli. We measured the average duration of a stable and uniform (single eye dominance) percept when a pair of locally orthogonal stimuli were presented dichoptically without between eye swapping. Previous studies have found that the alternation rate increases with stimulus size in both binocular and monocular rivalry (Mapperson & Lovegrove 1984; O'Shea et al. 1997; Andrews & Purves 1997) although this increase is also accompanied by a decrease in exclusive visibility periods and an increase in 'piecemeal rivalry' (Breese 1909; Blake et al. 1992; O'Shea et al. 1997). In our experiments, the effect of 'composites' and 'piecemeal rivalry' was minimal in all conditions. The accumulated duration of a single eye dominance was $96 \pm 1\%$ of the viewing time for the orientation jitter and size conditions and $90 \pm 4\%$ for the proximity condition, with no consistent relation between these small variations and any of the varied stimulus parameters. Thus, the average duration reflects the alternation rate as well. Results are shown in Fig. 2 (middle row), where for the three stimulus dimensions, durations decrease (rivalry speeds-up) with stimulus coherence. Rivalry of uniform textures was three times faster than for textures with orientation jitter and twice as fast as for spaced (4λ) textures or as for a single small patch. The effect was measured for three contrast levels (0.25, 0.5, 0.7) and the results show that higher contrast speeds-up the alternation rate, as previously found (Blake, 1989). However, the effects of contrast changes were much smaller than the configuration effects, which therefore could not be exchanged with contrast, or be accounted for by contrast-dependent saliency mechanisms. Indeed, non-coherent stimuli (with local orientation gradients) which we found to have slow alternation rate, were previously found to be more salient (Bonnef & Sagi, 1999) and have a higher perceived contrast (Cannon & Fullenkamp, 1991) than uniform stimuli.

3.4. Contrast invariance

Contrast is a known parameter in determining 'stimulus strength' in rivalry (Levelt, 1965) so that contrast differences between the eyes shift the relative dominance in favor of the higher contrast stimulus. We examined the way contrast interacts with stimulus coherence using static presentations (without swapping), where the contrast in one eye was kept constant (0.7) while the contrast in the other was set to either 0.25, 0.5 and 0.7, in a randomized order. Results are shown in Fig. 2 bottom row, with a separate plot for each contrast pair and for the three stimulus dimensions. A flat curve $\approx 50\%$ was expected for the identical contrasts (0.7/0.7). That was indeed the result (with some deviation, presumably due to differences between the eyes). However, contrast variation had only a small effect on coherent stimuli, but a very large effect on textures made of identical elements with jittered orientation or larger spacing and on a single small patch. In all these latter conditions, the higher contrast dominated almost the entire viewing time (80–90%). In addition, for non-coherent stimuli, the duty-cycle of both eyes changed, as opposed to coherent stimuli for which only the duty-cycle of the fixed-contrast eye decreased. Thus, non-coherent stimuli do not conform with the common finding that only the duration of suppression is affected by pattern contrast (Levelt, 1965; Blake, 1977; Logothetis et al., 1996). These results show that high global stimulus coherence entails a level of contrast invariance in rivalry. Moreover, if one accepts that lower levels of visual processing are contrast sensitive, while higher levels of processing are contrast invariant, these results suggest that globally coherent and incoherent stimuli are disambiguated at different levels of visual processing.

4. Discussion

Our results show that for stimuli rapidly swapped between the eyes, rivalry shifts gradually from eye-rivalry to pattern-rivalry when pattern coherence is increased. In addition, for non-swapped stimuli, increasing stimulus coherence results in two significant effects: coherent stimuli alternate faster and their relative dominance is less affected by contrast differences between the eyes. These results support the hypothesis that binocular rivalry involves competition at different levels of visual processing (Leopold & Logothetis, 1996; Wolfe, 1996; Ooi & He, 1999), from low-level eye-competition to higher level pattern-rivalry, depending on some stimulus parameters (such as orientation jitter) but not others (such as contrast). Our results show that both eye-rivalry and pattern-rivalry exist, as previously suggested by Wolfe (1996) and can co-exist at the same

time (Fig. 3) with a dynamic and stimulus-dependent balance between different eye- and pattern-specific mechanisms.

Two recent studies (Logothetis et al., 1996; Lee & Blake, 1999), both using the eye swapping paradigm, arrived at 'rival ideas about binocular rivalry' (Lee & Blake, 1999). Lee and Blake found a very narrow range of spatial frequencies (> 6 cyc deg⁻¹ for 50% contrast stimuli) and temporal frequencies (2.5–4 Hz for 50% contrast stimuli) over which pattern-rivalry occurs. Their results gave a much lower-estimate to the pattern-rivalry phenomena, possibly because their observers were asked to categorize the overall appearance of 10 s long displays, rather than continuously monitor the outcome of rivalry. However, Lee and Blake's finding that pattern-rivalry is spatial-frequency dependent is qualitatively consistent with our 'size' and 'spacing' dependencies, where lower-frequency stimuli have fewer cycles (size kept fixed) and thus, correspond to small and sparse ('non-coherent') stimuli, respectively, in the current study. The results of Logothetis et al. (1996) are consistent with our findings for coherent stimuli.

A critical issue in a multi-level explanation of rivalry concerns the nature of the ambiguity signal which presumably indicates to cells in binocular levels dichoptic from fused patterns. One attractive possibility is a temporal code (Freies, Roelfsema, Engel, König, & Singer, 1997; Lumer, 1998), with a temporal asynchrony between the two monocular signals suggested as a code for a mismatch (Lumer, 1998). Alternatively, it has been suggested that the selective activation of separate and not significantly overlapping populations of neurons, is the trigger for both binocular and monocular rivalry (Campbell, Glinisky, Howel, Riggs, & Atkinson, 1973a; Walker, 1976). Accordingly, the mismatch-signal could be coded by the lack of interocular cross-orientation integration, which causes an incomplete representation of non-fused stimuli. A dichoptic plaid, for example, might be represented as two orientations without their intersection, perceptual evidence for which has recently been reported (Georgeson & Meese, 1997). Having an 'ambiguity signal' other than an eye tag allows for rivalry to occur at different levels, such as the retinotopic and non-retinotopic rivalry recently found in strabismic patients (Ramachandran, Cobb, & Levi, 1994).

A second issue relates to the monocular level in rivalry. Our multi-level hypothesis suggests that the inconsistency signal stemming from the dichoptic input are propagated from low to high processing levels, where each level may contribute differently to resolve it. Thus, a small difference in the activity (level or synchronization) of a monocular cell population may serve to bias higher-level processing in favor of the stimulus coming from that eye. Based on the current findings, one can predict that this monocular signal will increase

for non-coherent stimuli, such as the random orientation texture. On the other hand, our results show that coherent stimuli can induce interocular integration across time and between-eye swaps, which extends the evidence for Gestalt based interocular grouping across space during binocular rivalry (Diaz-Caneja 1928; Wade, 1973; Kovács, Papathomas, Yang, & Feher, 1996).

A third issue concerns the source of the perceptual alternations in rivalry. The current findings (Fig. 2, center row) suggest that these alternations are related to an integration process, as coherent stimuli that are subject to perceptual integration and grouping alternated in a much faster rate as compared to non-coherent stimuli. One interpretation for this result is that the alternations in perception reflect the result of a cooperative process that produces global activity fluctuations. When the stimulus involves little integration, as in the case of random orientation texture, the local and unsynchronized fluctuations cannot initiate a global transition and each percept is 'stuck' in one state for longer periods. On the other hand, coherent stimuli initiate global transitions, which may involve large cortical networks across both hemispheres. The recent finding of inter-hemispheric switching in rivalry (Miller et al., 2000), suggests that each hemisphere 'adopts side' in these global alternations, but our results suggest that the role of hemispheric competition or any global transition mechanism in rivalry is expected to decrease for non-coherent stimuli.

Finally, it is important to note that the current results, which involve low-level type of stimulus, cannot be used to make claims about specific physiological 'levels'. A somewhat different interpretation of the data could, in principle, assign the different processing levels to the sensory areas V1, V2. This would be consistent with the recent finding of fMRI response in V1 that correlates with the perceptual alternation in rivalry (Polonsky et al., 2000) and with many studies that interpret perceptual integration as low level sensory mechanisms (e.g. Kapadia, Ito, Gilbert, & Westheimer, 1995; Bonneh & Sagi, 1999; Alais & Blake, 1999), but would be a challenge to any modeling scheme.

Taken together, our results support the hypothesis that binocular rivalry involves competition at different levels of visual processing (Leopold & Logothetis, 1996; Ooi & He, 1999) and, moreover, that the degree of global coherence of the stimuli presented to the two eyes can critically influence the level of processing at which the inconsistency is perceptually resolved. Indeed, we show that when different parts of the same stimulus are set at different levels of coherency (along parameters such as distance between elements of textures and orientation) the result is a coexistence of eye and pattern-rivalry for the corresponding parts of the stimulus. Thus, there might not be a single 'neural site

of rivalry' but rather the neuronal site or sites where the perceptual alternations are explicitly represented can shift in a stimulus dependent manner. A similar dynamic nature of awareness is perhaps indicated by clinical cases, that show that color contrast or local motion can induce awareness when the higher level processing stages (and thus, color constancy and global motion) are damaged (Zeki & Bartels, 1999). The possibility of multi-level allocation of awareness driven by lesion or by stimulus properties as we suggest, lends support to the notion of a hierarchical but potentially 'transparent' organization such that under specific (stimulus or lesion) conditions, activity at lower levels of the hierarchy comes to dominate awareness.

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