



Spatio-temporal dynamics of the visual system revealed in binocular rivalry

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Received 28 September 2004; received in revised form 23 January 2005; accepted 31 January 2005

Abstract

From the evolutionary viewpoint, animals need to monitor the surrounding environment and capture salient features, such as motion, for survival. The visual system is highly developed for monitoring a wide area of visual field and capturing such salient features. In humans and primates, there is a wide binocular field, suggesting a necessity of integrating the images from the two eyes. Binocular rivalry [R. Blake, A neural theory of binocular rivalry, *Psychol. Rev.* 96 (1989) 145–167; R. Blake, N.K. Logothetis, Visual competition, *Nat. Rev. Neurosci.* 3 (2002) 13–21], where incompatible inputs from the two eyes compete to emerge in the subject's visual percept, has been shown to exhibit highly adaptive behavior [I. Kovacs, T.V. Parathomas, M. Yang, A. Feher, When the brain changes its mind: interocular grouping during binocular rivalry. *Proc. Natl. Acad. Sci. U.S.A.* 93 (1996) 15508–15511; N.K. Logothetis, Single units and conscious vision, *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 353 (1998) 1801–1818]. Here we investigated the spatio-temporal dynamics of the ocular dominance pattern in binocular rivalry under conditions where conflicting salient features were presented in a temporally varying manner. We found a striking example of the detailed structure of the dominance wave propagation, by using a spatio-temporal sampling method. The data show in detail the ability of the visual system to dynamically adapt to the changing stimuli in the context of the massively parallel visual field. We show by model prediction that the globally coherent dominance change in the presence of multiple stimuli can be explained by a mechanism based on local saliency comparison.

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Keywords: Saliency; Binocular rivalry; Spatio-temporal sampling method; Dynamical adaptation

The visual system needs to monitor a wide area of visual field in a massively parallel manner, in order to enable perceptual grouping [26,31] and capture salient features embedded in the visual field. The difficulties inherent in dealing with massively parallel distribution of visual features in the wide visual field is demonstrated by the failures of the visual system to register salient features, in seemingly familiar situations such as those associated with inattention blindness [25].

The percept in the visual field is constructed as a result of a fusion of the inputs from the two eyes. In normal conditions, there is a high degree of correlation between the binocular signals, and fusion leads to depth perception. When the correlation between the binocular images is low, however, there

is a competition between the two eyes, resulting in binocular rivalry [4,5]. Studying the nature of binocular rivalry in the presence of competing salient stimuli is an effective tool for uncovering how the visual system captures salient features distributed in the visual field. Elucidating the neural correlates of binocular rivalry is also instrumental in clarifying the neural correlates of visual awareness [10].

The exact nature of neural mechanisms underlying binocular rivalry is not yet known. Signals from the right and left eye retinae are integrated at the primary visual cortex (V1), so the neural activities in area V1 are the obvious candidate for the neural correlates of perceptual alternation in binocular rivalry [4]. However, there are apparently conflicting reports.

The early psychological studies (e.g., [4]) and recent psychological [32] and imaging studies [16,24,28,30] seem to suggest that area V1 is crucial in inducing rivalry. On the

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other hand, the electrophysiological studies on binocular rivalry have suggested that the neural activities in the higher visual areas, such as area V5/MT, STS and IT, rather than area V1 were correlated with the subject's percept. Some other studies [15,19,29] also seem to support the latter view.

These conflicting evidences mainly arise from the fact that there are multi-level factors involved in competition between perceptual states, i.e., low-level sensory features and high-level cognitive interpretations [6,21]. In order to clarify the interplay between the lower and higher visual systems, we need to conduct a detailed analysis of the ocular dominance pattern in the spatio-temporal domain.

In spite of the knowledge of the existence of piecemeal rivalry [15,18,19], most studies on binocular rivalry have been conducted in an “all-or-none” paradigm, neglecting the spatial heterogeneity of ocular dominance pattern. Studying the dynamics in the spatial dimension is especially important in understanding the mechanism behind dominance change induced by temporally changing salient features. It is well known that the sudden onset of visual stimuli induces a perceptual alternation [11,33]. It is also known that the sudden onset of stimuli induces a dominance wave spreading from the locations of the onset stimuli. For example, Wilson and colleagues have studied the dominance wave propagation induced by a brief contrast change [32]. In general cases where there are more than one temporally varying features, the visual system must somehow assign dominance in the presence of competing sources of saliency, resulting in a highly complex dominance wave pattern.

At present, there are technical difficulties involved in monitoring the massively parallel adaptation of the visual system. Until a satisfactory model of the neural correlates of dominance change supplemented by a noninvasive measurement of neural activities is attained, we need to devise ways to obtain dominance data through the sequential motor output (i.e., key stroke) of the subject. Here, by applying a spatio-temporal

sampling method, we show that it is possible to reveal the detailed spatio-temporal structure of ocular dominance pattern in the full broadness of the visual field. We report here a striking case where two moving circles induce globally structured dominance wave propagation. It is shown by model prediction that computation based on local saliency comparison is sufficient to reproduce the dominance pattern. This result, taken together with earlier studies, provides insights into the neural mechanisms behind rivalry change, especially when a rich dynamics of dominance wave propagation is involved.

The subjects were three healthy adults with normal or corrected-to-normal vision (F.T., male, 24 years old, K.M., male, 37 years old, and I.I., male 30 years old). All subjects gave informed consent.

The stimuli used were one or two circle(s) moving on homogeneous background colors. The background colors were blue for the left eye and yellow for the right eye (Fig. 1a). These stimuli were chosen to investigate how the visual system can assign dominance to competing salient features in a dynamical manner. Preliminary observations have found that the ocular dominance pattern adapts dynamically to the moving visual stimuli and results in the representation of the salient features continuously. When the subjects were presented with two circles moving with various phase differences (Fig. 1a), they reported that both of the moving circles were continuously present in the percept. In the case of a phase difference of 180° , the subjects experienced a “flip-flop” change of the perceived background color. For phase differences other than 180° , the spatio-temporal ocular dominance pattern was often too complicated to be described from memory. In various phase difference conditions, the subjects reported always seeing both circles. When two stationary circles were presented in rivalry, sometimes either one or both of them disappeared from the percept (Fig. 1b).

We used a liquid crystal shutter eye wear (Crystal Eyes, Stereo Graphics Corporation, 2171 E. Francisco Boulevard,

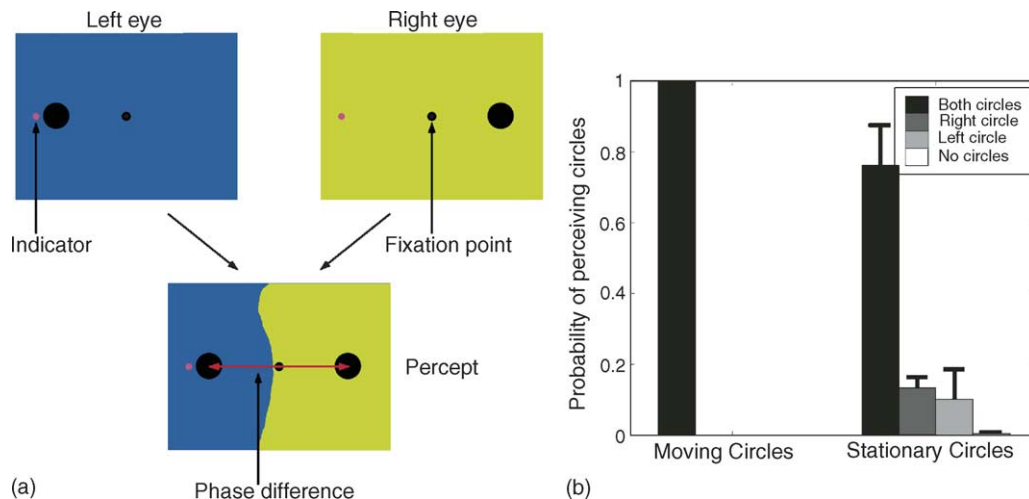


Fig. 1. (a) Experimental condition. The subjects were asked to fixate on the fixation point at the center of the screen. The circles move with a constant velocity of $4.4^\circ/\text{s}$. The subjects were asked to report by key pressing the background color at the position of the indicator that flashed with an interval of 1 s. (b) Average number of circles seen in the moving and stationary circles condition. Error bars show +1 S.D.

San Rafael, CA 94901, U.S.A.) with a dynamic range of 1000:1, to present the rivaling stimuli to the two eyes. The computer-generated graphics was presented on the monitor (Eizo E67T) with a frame rate of 120 Hz. The graphic converter extended the upper half and lower half of the graphics to the whole screen in alternating frames, with the left and right liquid crystal shutters being shut in an alternating fashion in synchrony with the screen. An infrared emitter synchronized the liquid crystal shutters. We presented the visual stimuli by using customized software running on a PC (Endeavor Pro-400L, Epson).

The image was projected on a computer screen (22° (horizontal) and 16.6° (vertical) in visual angle). The subjects were instructed to fixate on the center (Fig. 1a). The circles were 1.4° in diameter, and moved with a constant velocity of $4.4^\circ/\text{s}$. This angular velocity was chosen so that the subjects experienced robustly the typical background color percept change. When the edge of the circle reached the border of the screen, the circles reversed their directions and continued to move with a constant velocity in the opposite direction.

Because of the effect of cortical magnification, the effective area of cortex being stimulated by the circles change depending on the eccentricity. However, we chose to keep the physical sizes of the circles constant in order to reproduce commonly occurring situations in natural scenes. We note that the propagation speed of traveling waves of dominance is unaffected by cortical magnification [32]. There is a well-documented temporal hemifield advantage in rivalry [27], and this could possibly affect the result. However, in our experiment, there was not a significant tendency for a more pronounced dominance of the ipsilateral color when the moving circles were in temporal hemifield than the nasal hemifield. Contours and textures in the background could affect the resulting dominance pattern. Preliminary experiments suggest that the existence of grating pattern in the background, for example, can affect the resulting dominance pattern induced by the moving circles. Our present condition, therefore, represents the case of the most simple background pattern.

In order to study the detailed spatio-temporal dominance pattern, we conducted an extensive sampling study. During the presentation of the stimuli, an indicator was presented at one of the five equally spaced positions in the line of the motion of the circle center. The indicators were at 3.7 , 7.3 , 11.0 , 14.7 and 18.3° from the left edge of the screen, at an interval of 1 s. The subject answered the perceived background color at the position of the indicator by pressing one of two specified keys in a two alternative forced choice between two colors. The key input was recorded and analyzed on the PC. The probabilities are resampled using the bicubic interpolation method [13].

The positions and timing were chosen so that the indicator never overlapped with the circles. The indicator was flashed 50 times in one trial. We conducted five trials for each set of values of phase difference (0 , 72 and 180°) and indicator position. Thus, the subject reported the perceived color at 250

points in the spatio-temporal domain in one trial. As depicted in Fig. 3, where red and blue lines indicate the trajectories of circles, in the case of phase difference of 180° (Fig. 3a), the circles always move in the opposite directions. On the other hand, in the case of 72° (Fig. 3b), the circle presented to the left eye (red line) always follows the circle presented to the right eye (blue line). In the case of 0° (data not shown), two circles move together, thus they are seen as one circle in effect. In the stationary circles condition, the position of the circles were taken to represent the snapshots of presented image in the 180° phase difference condition at the moment of the indicator presentation.

The physical configuration of the crystal shutter eyewear made it difficult to monitor the subject's fixation at the time of the experiment. As an indirect control, we measured the subject's point of fixation by using the eye tracking system (EMR-8, NAC Image Technology, 15 McCoy Place Simi Valley, CA 93065 U.S.A.) as the image of two moving circles in a homogeneous color background (blue) were presented binocularly (i.e., no rivalry involved). The point of gaze stayed within 1.5° of the fixation point for 98.7 and 90.1% of the time for the x - and y -axis, respectively (mean of F.T. and one additional subject). The informal post-experiment reports by the subjects suggested that the resulting dominance patterns were not greatly affected by small deviations of the point of gaze.

In order to investigate the common neural mechanism involved in the percept change in the single circle and double circles condition, we made model predictions for the double circles condition from the data in the single circle condition. Predictions for the double circles condition from the single circle data were made by calculating the average probability of dominance assuming that the double circles condition can be approximated by a linear combination of the single circle conditions, where one circle is moving in the left eye image, the other moving in the right eye image, with the predetermined phase difference value.

Thus,

$$p(E, \{L, R\}) = \frac{p(E, \{L\}) + p(E, \{R\})}{2}$$

Here, $p(E, S)$ indicates the probability of $E = \{L, R\}$ eye dominance, where L indicates left and R indicates right, during presentation of circle to $S = \{\{L\}, \{R\}, \{L, R\}\}$ eye(s).

Fig. 2a shows the spatio-temporal structure of ocular dominance pattern reported by subjects when presented with a single circle moving in a blue background (presented to the left eye) against a homogeneous yellow background (presented to the right eye). The left eye dominant region is distributed in the vicinity of the moving circle presented ipsilaterally, implying that not only the moving circle itself but also the ipsilateral regions in the vicinity of the circle tend to win over the contralateral regions ("vicinity" effect). The left eye dominance is invoked with a certain amount (~ 0.7 s) of temporal delay, in a traveling wave of dominance lagging behind the circle. Once the left eye dominance for a particular position

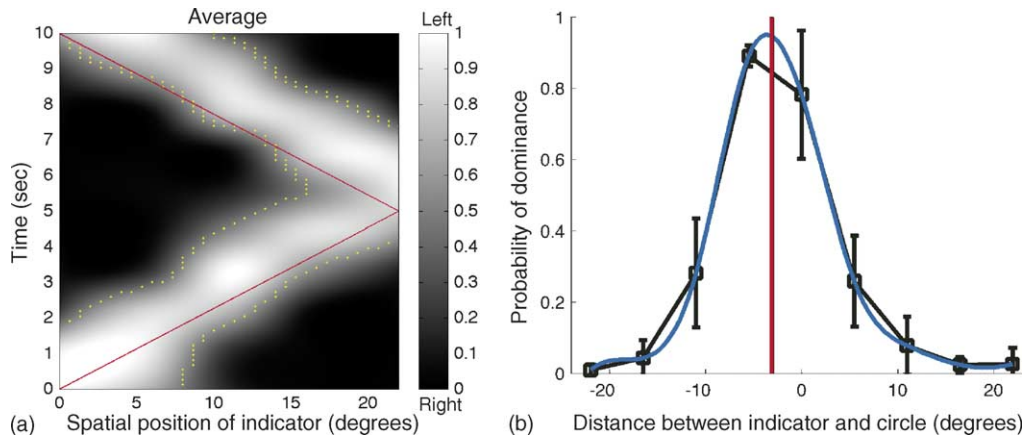


Fig. 2. (a) The spatio-temporal structure of ocular dominance pattern during the presentation of a single circle averaged over three subjects. The gray scale indicates the ocular dominance probability. Red line represents the trajectory of the moving circle presented to the left eye. Yellow dots represent the 0.5 chance level. (b) Time course of the ocular dominance change for the average of three subjects during the presentation of a single circle. Here, we show the probability of perceiving the ipsilateral color, as a function of the distance from the center of the moving circle. The blue line indicates the interpolated data by means of cubic spline interpolation method, while the red line indicates the point (-3.1° in visual angle) which divide the area surrounded by blue line into two equally sized parts, suggesting an average temporal delay of 0.7 s in the ocular dominance change. Error bars show +1 S.D.

in the visual field is over, right eye dominance is more likely (fatigue effect) [7].

Fig. 2b shows the probability of perceiving the ipsilateral color as the function of the distance between the indicator and the center of the single circle. The data set used are the same as for Fig. 2a. As can be seen from the figure, the ipsilateral color dominance follows rather than precedes the moving circle. Note that the diameter of the circle is 1.4° . There is an almost exclusive dominance of the ipsilateral color after the passage of the circle, with the domain of >0.8 probability of dominance estimated to extend for 6.2° .

Fig. 3a shows the spatio-temporal structure of ocular dominance pattern when the subjects were presented with two moving circles in homogeneous color backgrounds with a phase difference of 180° . When the moving circles cross over at the center of the visual field, the left eye and the right eye dominant regions “flip” their positions. Fig. 3b shows the

dominance pattern when the phase difference = 72° . Here, the spatio-temporal structure is much more complicated, but the background color percept still changes in a way so that both circles are continuously present in the percept.

As the sampling method reported in this study involves only one spatial dimension, we cannot reproduce the dominance change in the fullness of the two dimensional visual field. In the case where two circles are presented with 180° phase difference, the subjects’ verbal reports suggest that the dominance changed in a “flip-flop” like manner as depicted in Fig. 1a, with the dominance spreading distally from the line of motion of the circles. When the two circles move with other phase differences and in the single circle condition, the dominance in general has a tendency to spread distally from the line of motion, so that a “comet-like” narrow dominance tail lagging behind the moving circle(s) was not observed.

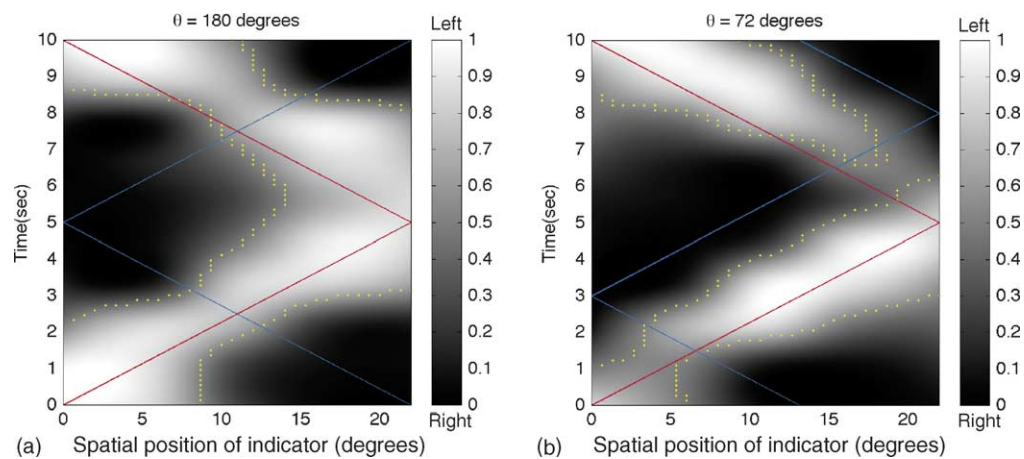


Fig. 3. Spatio-temporal structure of ocular dominance pattern during the presentation of the two circles moving in a homogeneous color background, with a phase difference of (a) 180° and (b) 72° . The gray scale indicates the ocular dominance probability. Red lines represent the trajectory of the moving circles presented to the left eye. The blue lines represent the one for the right eye. Yellow dots represent the 0.5 chance level. Averaged over three subjects.

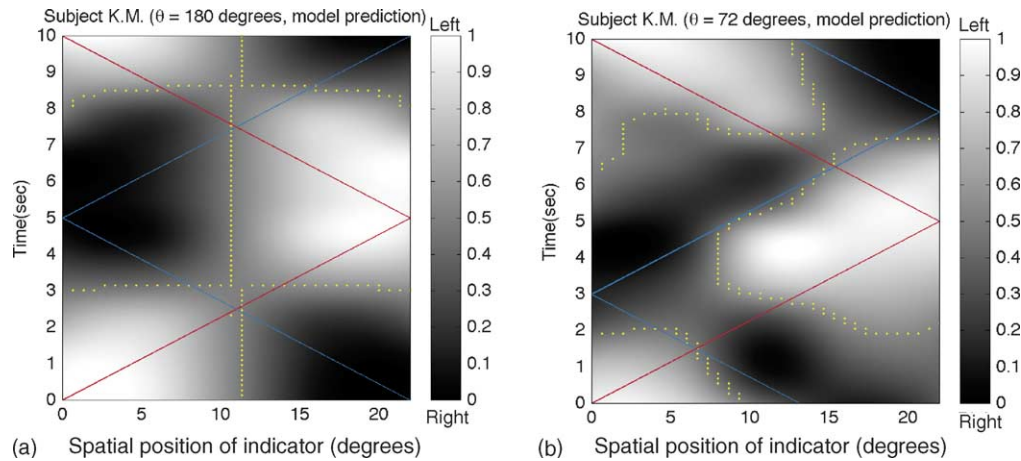


Fig. 4. The ocular dominance pattern in the double circles condition predicted from the single circle condition, with a phase difference of (a) 180° and (b) 72° . The data are shown for subject K.M.

In order to examine the relation between the single circle dominance pattern of Fig. 2a and the double circles dominance pattern of Fig. 3, we tested how one could predict one from the other. Fig. 4 shows the model predictions for the dominance probability for subject K.M. in the double circle condition predicted from the data of single circle. When sampled over 33 (spatial) \times 73 (temporal) = 2409 (spatio-temporal) points, for subject K.M. the predicted value was off the actual value by an average of 8.2 and 18% for the phase difference of 180 and 72° , respectively. For the average of three subjects, the mean difference between the predicted and actual data were 8.2 and 17% in the case of 180 and 72° phase difference, respectively. Thus, we conclude that the spatio-temporal structure of ocular dominance pattern in the single circle and double circles conditions were fairly consistent, suggesting a common underlying neural process.

Experiments with varied speed of the moving circles would facilitate further understanding of the cortical mechanisms involved. Preliminary results suggest that the continuous presentation of two circles in the percept is quite robust over different velocity of the circles.

Binocular rivalry is a competition not only between right and left eye [4], but also between features [15,19], leading to alternative interpretations of the external world. Alais and Blake [1] reported that the globally coherent motion stimuli enhanced the predominance of the local motion stimuli. Ooi and He [22] suggested that the voluntary attention could influence the visual perception only during dominant phase. These observations, taken together with our data, point to a highly complex dominance assignment process in the presence of dynamically changing salient features. The delay of ocular dominance change in single circle condition (Fig. 2) may reflect the time required for object-based mechanism to work [21].

In double circles conditions, the visual system behaves as if it can predict the trajectory of moving circles, in spite of the lack of prediction in single circle conditions. Barlow [3] has pointed out that “prediction is possible if there is spatio-

temporal redundancy in the input data”. The fatigue after passing of circles moving in a periodic manner is a possible neural mechanism for exploring redundancy. This temporal alternation of the percept might also reflect the “inhibition of return” (IOR), the process by which the currently attended location is prevented from being attended again [12,14]. Recent studies have suggested that perceptual alternation in binocular rivalry and ambiguous figures share a common mechanism [2,9,17,18]. The “flip-flop” effect observed in the double circles condition might reflect such a temporal integration [23].

Although the spatio-temporal ocular dominance pattern in the presence of two moving circles is quite complex, the fairly good model prediction of ocular dominance pattern in double circles conditions from that in single circle conditions (Fig. 4) indicates that the dynamics of ocular dominance change, such as “flip-flop” effect might be explained by the fatigue after passing of the salient features, suggesting that the relatively rapid change may be caused by the interaction within neurons in the lower visual areas, such as V1. Two factors, namely the induction of dominance by a moving stimulus, and the fatigue after the passing of the dominance, seems to explain the spatio-temporal dominance pattern in the single circle and double circles conditions. Within the set of competing salient features studied here, local nonlinear dynamics seems sufficient to explain the dominance wave propagation.

Carlson and He [8] have revealed that conflicting global stimuli that consist of compatible local elements failed to induce binocular rivalry, implying that the initiation of rivalry occurred at an early stage of visual processing. Our present analysis of dominance wave also suggests that the globally structured dominance change reported here can be explained by local nonlinear dynamics, suggesting the involvement of early visual system. Although the involvement of higher visual areas in general cannot be excluded, we suggest that a local computation supported by early visual areas can result in a highly rich dynamics of dominance wave propagation.

We have shown here that a conventional psychophysical method, implemented with an appropriate spatio-temporal

sampling paradigm, can reveal the detailed spatio-temporal structure of the ocular dominance in binocular rivalry. Such a method would provide a window to the functionally embedded dynamics of the visual system, especially when combined with the brain imaging techniques such as fMRI and MEG [20,24,28–30].

Acknowledgement

We thank Dr. Mario Tokoro for helpful discussions. We are indebted to the two reviewers for valuable comments.

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