



Dynamical systems modeling of Continuous Flash Suppression

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ABSTRACT

Continuous Flash Suppression (CFS) is a technique in which a stationary image in one eye can be reliably suppressed by rapid presentation of different flashing images in the other. In this paper we address why flashing stimuli modulate the visibility of the stimuli. We determine, in particular, which type of neural network is sufficient for the modulation of the dominance duration, assuming that elemental units are endowed with reciprocal inhibition and adaptation. We show that the model introduced by Wilson (2007) reproduces flash suppression, which is considered to be involved in CFS, but does not reproduce CFS. We then extend the model by including a stimulus feature dimension. With this extension, we found that the model accounts for the modulation of visibility observed in CFS. In addition, this model captured some defining characteristics of CFS such as dependence on flash interval and the depth of suppression. Our findings suggest that a network with inhibition and adaptation including feature dimension provides a crucial mechanism for the modulation of the dominance duration in CFS.

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1. Introduction

Binocular rivalry has shed light on the dynamics of visual awareness and its underlying neural basis. In the study of this phenomenon, a method termed Continuous Flash Suppression (CFS) has been recently devised (Tsuchiya & Koch, 2005). This technique delivers continuously flashing images to one eye while a stationary image is presented to the other eye. A remarkable phenomenon in CFS is that it elongates the dominance duration (DD) of the percept of the flashing stimulus in CFS regime compared to the DD in binocular rivalry (BR). At the same time, the flashing stimulus shortens the DD of the percept of the stationary stimulus compared to the DD in BR. As a result, the flashing stimulus is perceived for a longer period than the stationary stimulus. The flashing images thereby modify the observer's visual perception. While Tsuchiya and Koch used fragmented and contour-rich visual stimuli in their CFS experiment, it is known that features of stimulus patterns such as color and high-dimensional texture are not critical for the suppression of a stationary image. Indeed, the suppression of a stationary image is induced even with the simple monochrome stimulus set as adopted by Gilroy and Blake (2005). Rather, the flash interval

profoundly modulates the perceptual dominance, as reported in Tsuchiya and Koch (2005, Supplementary info).

CFS is now used as an established technique in psychophysical and fMRI experiments for its strong effect on perceptual dominance (Fang & He, 2005; Gilroy & Blake, 2005; Jiang, Costello, Fang, Huang, & He, 2006; Jiang, Costello, & He, 2007; Pasley, Mayes, & Schultz, 2004), especially to investigate the relationship between subjective perception and retinal aftereffect (Tsuchiya & Koch, 2005). However, few studies (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006) have addressed why stimulus flashing renders the stationary image invisible. It is important to elucidate underlying neural mechanisms of how the flashing stimulus modulates perceptual dominance, for determination of the relationships between visual awareness and neural dynamics. Since the retinal aftereffect is primarily occurring in the retina, whereas the visual rivalry takes place in the cortex, the neural mechanisms underlying these two phenomena are distinct, and should be separately addressed.

In the study of multistable perception, several studies have proposed neural mechanisms which account for spontaneous rivalry alternation. Most of models have employed both reciprocal inhibition between competing neural groups and adaptive suppression of neural activity over time. By means of these mechanisms, a group of neurons maintains transient dominance until the activity of the competing group can no longer be inhibited, leading to a switch of perceptual dominance. These mechanisms are now supported in part by psychophysical and fMRI studies (Lankheet, 2006; Tong & Engel, 2001). Lankheet (2006) succeeded in extracting adaptation and mutual inhibition components in rivalry, while Tong and Engel (2001) provided evidence for inhibition of activity in V1 monocular neurons during rivalry.

Abbreviations: BR, binocular rivalry; FS, flash suppression; CFS, Continuous Flash Suppression; DD, dominance duration; sDD, dominance duration of the percept of the stationary stimulus; fDD, dominance duration of the percept of the flashing stimulus.

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Based on these observations, we hypothesize that adaptation and reciprocal inhibition are involved in CFS, especially in the modulation of DD by the flashing stimuli. By using reciprocal inhibition and adaptation as composition elements, we investigate the requisite neural-network architecture of CFS. Here we adopt a simple model, because our focus is on capturing the essential neural mechanism underlying CFS. Specifically, we examine a minimal model introduced by Wilson (2007) that implements reciprocal inhibition and self-adaptation.

First, we examine the response of Wilson model to a single flash of stimulus to test whether the model reproduces flash suppression (FS), which is thought to be required in CFS. FS is the perceptual suppression of a monocularly presented image, upon flashing of a new stimulus to the contralateral eye (Wolfe, 1984). We subsequently examine the model’s response to a continuously flashing input as employed in CFS experiments and show that the response is opposite to that observed in CFS experiments. To reproduce the experimental results, we extend the original model so that it can deal with feature dimensions of visual stimuli. In the extended model, the flashing stimulus remarkably elongates its DD and shortens that of the stationary image. In addition, we show that this extension also reproduces the dependence of DD on the flash interval, a unique characteristic of CFS. Finally, we investigate a model with more units, confirming that the suppression of CFS is far stronger than that of FS and BR.

2. Model

2.1. Wilson model of binocular rivalry

Wilson (2007) introduced one of the simplest models of BR that implemented competitive inhibition and self-adaptation. Despite its simplicity, the model can reproduce Levelt’s second and fourth law (Levelt, 1966). This model is composed of four variables, namely E_L, E_R, H_L and H_R . E_L (E_R) represents the activity level of neurons driven by the left (right) monocular inputs $L(t)$ ($R(t)$), whereas H_L (H_R) stands for a slow hyperpolarizing current injected into E_L (E_R). The temporal evolution of the four variables are described as

$$\tau \frac{dE_L}{dt} = -E_L + M \cdot \max(L(t) - aE_R + \varepsilon E_L - gH_L, 0),$$

$$\tau_H \frac{dH_L}{dt} = -H_L + E_L,$$

$$\tau \frac{dE_R}{dt} = -E_R + M \cdot \max(R(t) - aE_L + \varepsilon E_R - gH_R, 0),$$

$$\tau_H \frac{dH_R}{dt} = -H_R + E_R.$$

The meanings of the parameters are fully explained in Wilson (2007), Table 1. Unless otherwise noted, the system parameters are set as $dt = 0.01$ ms, $\tau = 20$ ms, $\tau_H = 900$ ms, and $R = 1$. Most of the other parameters are chosen as supplied in Table 1 of Wilson (2007).

We briefly review basic behaviors of the model with constant stimuli ($L(t) = L, R(t) = R$). The system has two fixed points and their stability depends on the parameter values (Wilson, 2007). Fig. 1 illustrates how the model’s behavior depends on values of the parameters L/R and a . The boundaries of the regions in the parameter space depicted in the figure are represented by the following inequalities (The deviation of these inequalities and full description of the behavioral patterns are found in Wilson (2007)),

$$a > \left(g + \frac{1}{M} - \varepsilon\right) \frac{R}{L}, \tag{1}$$

$$a > \left(g + \frac{1}{M} - \varepsilon\right) \frac{L}{R}, \tag{1' equation}$$

$$a < \frac{1}{M} - \varepsilon, \tag{2}$$

$$a > \left(\frac{1}{M} - \varepsilon\right) \frac{L}{R}, \tag{3}$$

$$a > \left(\frac{1}{M} - \varepsilon\right) \frac{R}{L}. \tag{3' equation}$$

Since switching of perceptual dominance in binocular rivalry is highly stochastic even under well-controlled experimental conditions, effects of noise should be taken into account. Indeed, under the presence of noise, Wilson model reproduces a gamma distribution of DD, which is a typical characteristic of binocular riv-

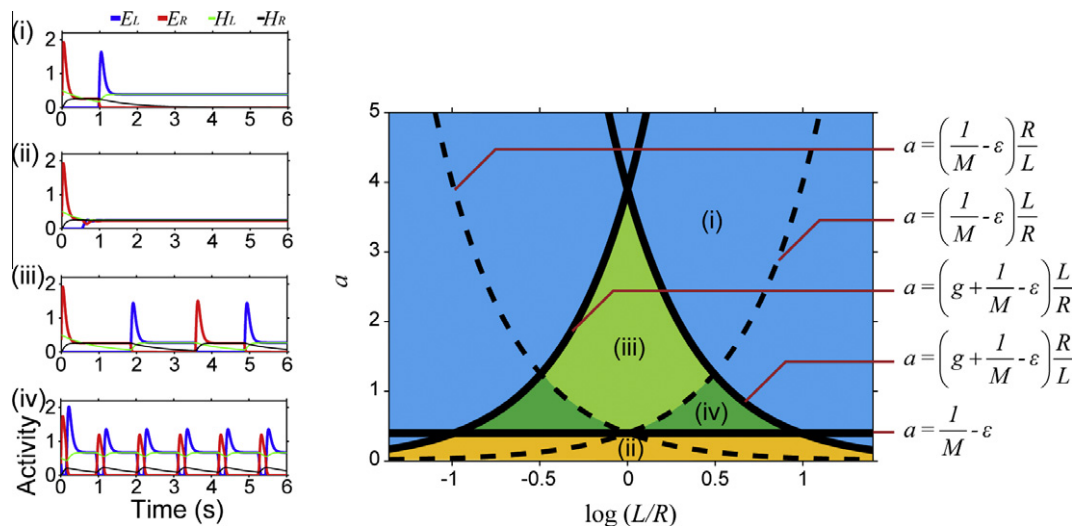


Fig. 1. Basic behavioral patterns of Wilson model in response to stationary inputs in L/R - a parameter space. The time course of each behavioral pattern is demonstrated in the left four figures. (i) E_R - or E_L -fixed point (winner take all) at which E_R or E_L continues firing. (ii) Both-firing fixed point (fusion) at which both E_R and E_L continue firing. (iii) Limit cycle (binocular rivalry) in which dominance switches when H_R or H_L reaches close to its asymptote. (iv) The other limit cycle in which dominance switches long before H_R or H_L reaches its asymptote.

alry. The importance of noise in binocular rivalry is further discussed in Moreno-Bote, Rinzel, and Rubin (2007). For these reasons, we examine the model with weak Gaussian white noise in the following simulations.

3. Results

3.1. Time-lagged input to Wilson model switches dominance over wide parameter region

Before investigating the model response to repetitive flash, we inquire whether a single flash of input switches the dominance of neural activity in Wilson model. For this purpose, we first present a monocular (stationary) stimulus to one eye of the model and then give another monocular stimulus to the other eye. The interval between the two stimulus presentations is 2000 ms, which is sufficient for the slow variable, i.e. H_R or H_L , to reach its asymptote. We examine whether the response of neural activity to the second stimulus is dominant compared to that to the first stimulus. In particular, the parameter region is examined in which the dominance switches immediately after the second stimulus.

Fig. 2 illustrates the parameter region in which the model behaves like FS (without the loss of generality, we presented the first stimulus to the right eye and the second stimuli to the left). The FS-like behavior is observed over a wide area including where binocular rivalry takes place in response to a normal stationary stimulus.

The parameter region of FS-like behavior can be captured by the following arguments obtained with the use of the adiabatic approximation before and after the time-lagged input. If $a > (g + \frac{1}{M}) \frac{R}{L}$ is satisfied, the E_R -fixed point vanishes upon the delivery of the second input to E_L . Once the system leaves the vanished fixed point, it moves toward either of the newly appearing fixed points $(E_L, E_R) = (ML, 0)$ and $(\frac{MR - aM^2L(1+Mg)}{(1-a^2M^2)(1+Mg)}, \frac{ML(1+Mg) - aM^2R}{(1-a^2M^2)(1+Mg)})$, depending on the parameter values. If $a > \frac{1}{M(1+Mg)} \frac{R}{L}$ is satisfied, the system is attracted to the E_L -fixed point. However, if $a < \frac{1}{M(1+Mg)} \frac{R}{L}$ and $\frac{1}{1+Mg} < \frac{L}{R}$ are satisfied, the system is attracted to the bi-firing fixed point where E_L is larger than E_R .

3.2. Repetitive flashing input shortens fDD of Wilson model

We next investigate whether repetitive flashing of input modifies DD as observed in experiments of CFS. In CFS experiments of

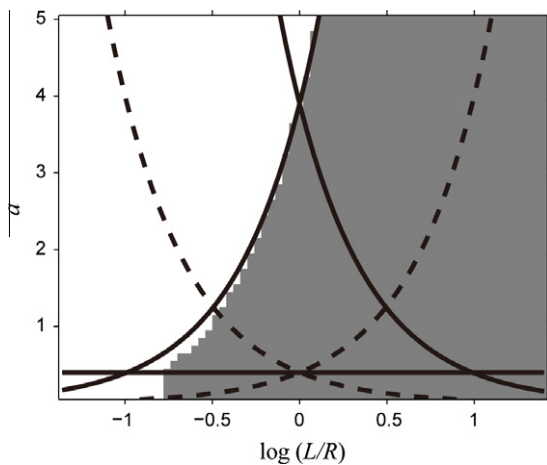


Fig. 2. The responses of Wilson model to time-lagged input in the L/R - a parameter space. The region where Wilson model changes dominance from right (unit with the first stimulus) to left (unit with the second stimulus) within 100 ms is marked with gray. Transient switches in the dominance are included to be FS without reference to the subsequent behavior. Noise = 1.0×10^{-6} . With a deterministic simulation, nearly the same diagram is obtained.

Tsuchiya and Koch (2005), fragmented, contour-rich patterns (known as Mondrian pattern) were exploited as flashing stimuli. However, rather simple stimuli of a monochrome pinwheel and its contrast reversed version induce basically the same features of CFS, including suppression of visibility of the stationary stimulus and reduction of after-image intensity for the stationary stimulus (Gilroy & Blake, 2005). Since such flashing inputs have distinct patterns at every flash, optimality of pattern for eliciting firing by a group of neurons changes from pattern to pattern. Thus, after a flash at a given time elicits the maximum response of a group of neurons, the subsequent flash often yields little or no response. Therefore, focusing on the temporal structure of the stimulus used, we set the external stimuli $L(t)$ and $R(t)$ so that the stimuli to one eye remain unchanged while those to the other eye continue changing between on and off.

To examine the response of the model to the flashing input, the interval of the flash should be taken into account, since the previous experiment (Tsuchiya & Koch, 2005) reported that the flash interval substantially affected DD. Fig. 3a is a graph adopted from Supplementary info of Tsuchiya and Koch (2005) showing that the DD of the flashing input is longest when the stimulus flash interval is 80–320 ms, and that the flashing input does not otherwise increase the DD. To replicate this experimental condition, Wilson model was presented with flashing input for 60 s in four different trials. We set stimulus strength for the flashing input weaker than that for the stationary input, and measured the mean and total DD of flashing and stationary stimuli.

Fig. 3b shows how flash interval modulates DD of flashing and stationary stimuli, which are hereafter referred to as fDD and sDD, respectively. In contrast to Fig. 3a, fDD (blue lines) is always shorter than sDD (red lines). Although we ran the simulations over a wide range of the L/R - a parameter values, we did not observe the modulation of DD observed in CFS experiments. The same tendency is observed when we employ other input patterns such as sinusoidal wave instead of the rectangular input. These results indicate that, in Wilson model, continuous flash does not lead to the suppression of visibility of a stationary stimulus. Note that this failure is not surprising given the fact the model deals with only the subset of neurons that responds to a part of the flashing input. In the simulations we frequently observed that dominance switches from the flashing stimuli to the stationary stimulus during a stimulus-off period of the flashing input sequence. This observation suggests that fDD is not so large because the unit that receives the flashing input cannot maintain dominance during the stimuli-off period.

3.3. Extension of Wilson model accounts for visibility modulation by the flashing stimulus

In this section we add a slight extension of Wilson model. To check whether the extension of the model explains the corresponding experiment, we particularly investigate dependence of DD on the flash interval. To verify that the flashing input modulates DD over a wide parameter region, the extended model is examined under the L/R - a parameter domain.

We have thus far focused on the temporal structure of the stimuli in CFS experiments, ignoring the effect of stimulus feature. This stimulus feature, however, may play a crucial role. For example, Mondrian flashing patterns, which are often employed to elicit CFS, have a fragmented, non-uniform spatial structure. One way to introduce stimulus feature in Wilson’s framework is to add other units that respond to different stimuli than that preferred by existing units. As a simple extension of the model, the case of two units in each eye is depicted in Fig. 4a.

This extension leads to the following differential equations

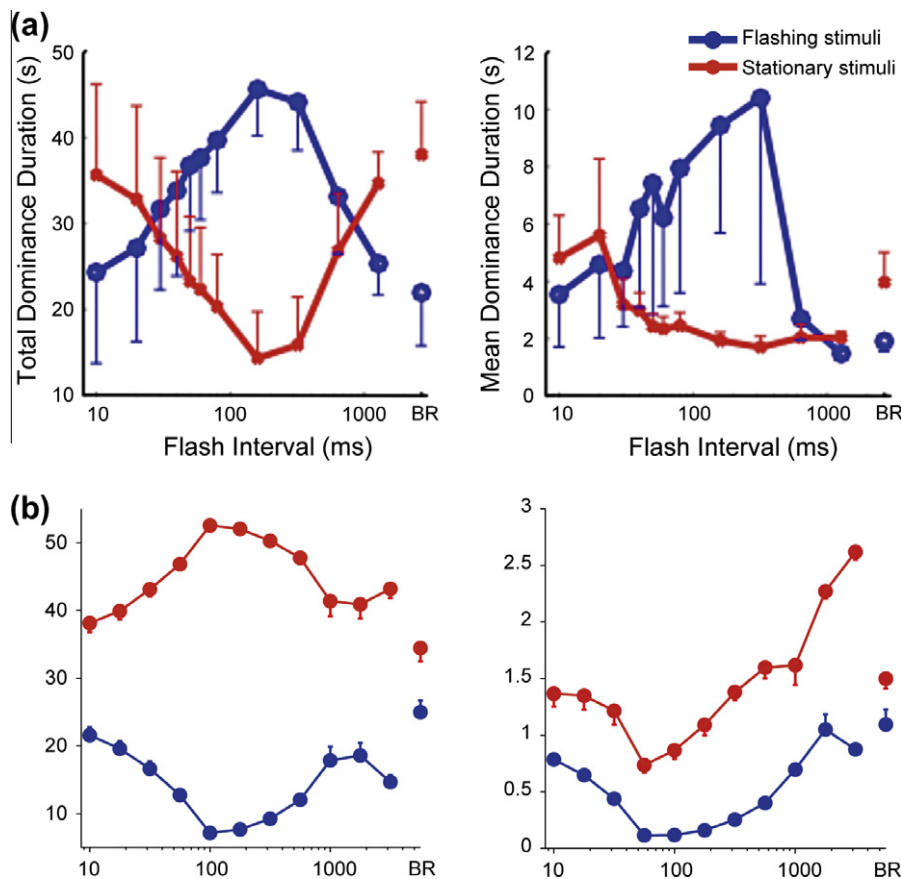


Fig. 3. Comparison of DDs between (a) data from a psychophysical experiment (Tsuchiya and Koch (2005), Supplementary note) and (b) the numerical results for Wilson model. In each figure, the red lines represent sDD while the blue lines represent fDD. The rightmost two points are for the case of binocular rivalry. In (a), four subjects tracked the visibility of a stationary stimulus during 1 min in four different trials viewing when any part of the stationary stimulus was visible (red) or invisible at all (blue). Error bars represent standard error across the trials. In (b), stimulus strength for the left unit is 0.9, while that for the right unit is 1.0. Error bars represent standard deviation. The system parameters are: $a = 4.0$, $g = 3.5$, $\varepsilon = 0.0$, $M = 1.0$ and Noise = 5.0×10^{-7} . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$\begin{aligned} \tau \frac{dE_{L1}}{dt} &= -E_{L1} + M \cdot \max(L_1(t) - aE_{R1} - a_2E_{R2} - gH_{L1}, 0), \\ \tau_H \frac{dH_{L1}}{dt} &= -H_{L1} + E_{L1}. \end{aligned} \quad (4)$$

(E_{L2} , H_{L2} , E_{R1} , H_{R1} , E_{R2} and H_{R2} are defined in the same fashion.)

The point of the extension is that each unit on one side receives different input (such as L_1 and L_2). Thereby the extended model can represent each unit as tuned to different stimulus features such as spatial phase, orientation, and color. For example, when external input (L_i , R_i) stands for sinusoidal images of different spatial phase, the corresponding unit can be interpreted as a group of V1 simple cells in which the neurons respond to particular spatial phase (Fig. 4a).

In this model, each unit receives inhibitory synaptic input with strength a_2 , in addition to the input with strength a in the original model. In this study, we adopt $a_2 = a$ for simplicity. The effect of a_2 on DD will be discussed in the subsequent section.

To examine the effect of stimulus flashing in our extended model, we set the input to one eye as stationary and that to the other eye as anti-phase flashing inputs as illustrated in Fig. 4c. Each of the flashing inputs has the form of an on-off rectangular wave, with constant flash intervals and strength. We test whether fDD is longer than the corresponding DD in BR, based on the definition that the sum of the activities of the two units for one eye stands for the activity that determines the dominance of the eye.

Results of simulation for a typical parameter set are demonstrated in Fig. 4b and c. The figure shows that the activities with

flashing inputs oscillate at the frequency of the external inputs (10 Hz). The sum of these activities maintains their dominance (fDD) for twice as long as DD in BR (blue, right most point). At the same time, sDD decreases to less than half of DD in BR (red, right most point). Consequently, fDD is much larger than sDD, even though the stimulus strength of a flashing stimulus (0.9) is set weaker than that of the stationary stimulus (1.0).

We subsequently examine the dependence of DD on flash interval in the extended model. The model was presented with flashing input for 60 s in four different trials to replicate the experimental conditions, while the mean and total DDs were measured. Fig. 5 shows results of simulation for a typical parameter set. Dependence of DD on the flash interval is characterized by two features. First, when the flash interval is less than 50 ms, the total and mean fDD (blue lines) are nearly four times larger than DD in BR. At the same time, the mean sDD (red line) is held constant below DD in BR. Consequently, the fDD is longer than that of sDD, even though the stimulus strength of the flashing input is weaker than that of the stationary input. Second, when flash interval increases more than 50 ms, fDD decreases to be close to DD in BR designated at the right edge. Similarly, sDD increases to approach DD in BR.

These two effects of flashing input on DD are more pronounced, when the strength of inhibition between the diagonal units a_2 is set larger. If a_2 is small enough, the effects are diminished since the system is reduced to the original Wilson model. To conclude, the modulation of DD as a function of flash interval is captured by a simple and minimal extension to Wilson model. The only

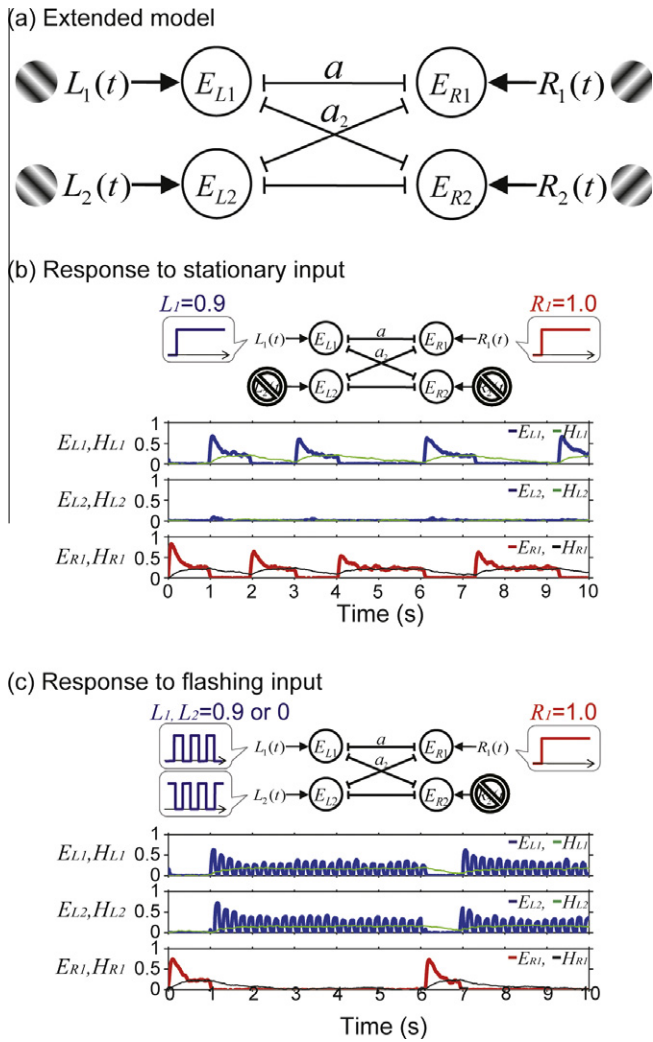


Fig. 4. (a) Architecture of the extended model. Two units on one side represent position in feature space. (b and c) Time courses of response in the extended model to (a) stationary inputs to both sides and (b) stationary input to one side and flashing stimuli to the other side. Note that E_{R2} and H_{R2} are almost always zero throughout. The system parameters are: $a = a_2 = 4.0$, $g = 3.5$, $\varepsilon = 0.0$, $M = 1.0$, $\varepsilon_2 = 0.0$, noise = 5.0×10^{-7} and flash interval = 100 ms.

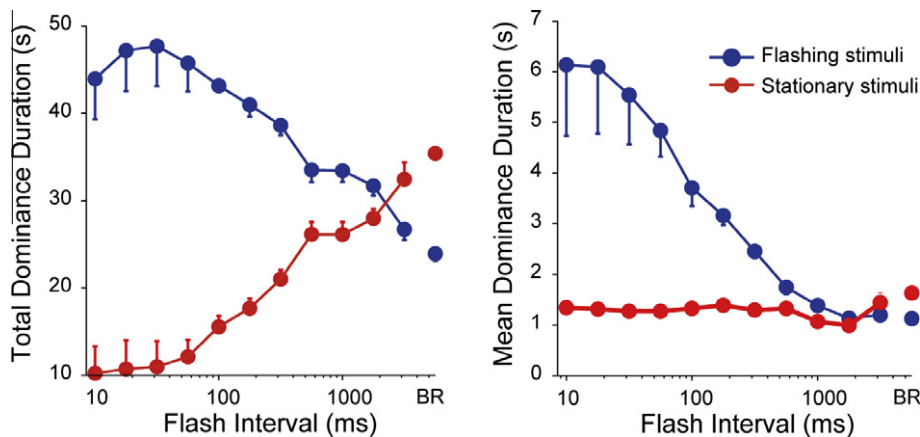


Fig. 5. Total and mean DDs for the extended model are plotted as a function of flash interval. In each figure, the red lines represent sDD while the blue lines represent fDD. The rightmost two points are for the case of binocular rivalry. Numerical results are obtained from simulation for 60 s \times 4 trials. Error bars represent standard deviation across the trials. Stimulus strength for the left units is 0.9, while that for the right units is 1.0. The system parameters are: $a = a_2 = 4.0$, $g = 3.5$, $\varepsilon = 0.0$, $M = 1.0$ and noise = 5.0×10^{-7} . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

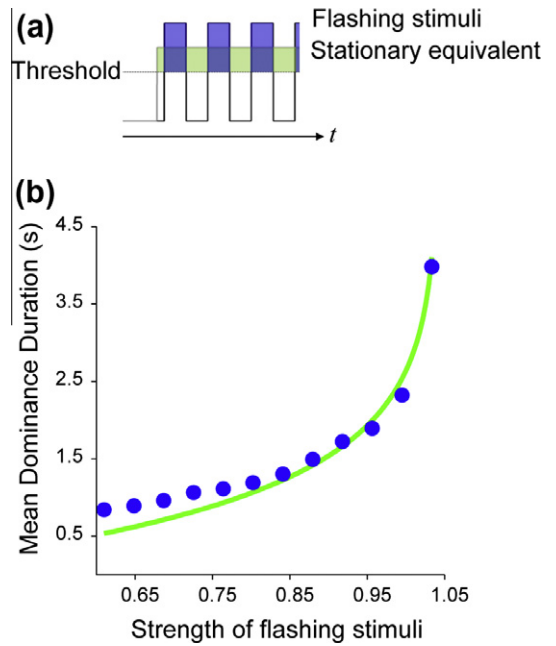


Fig. 6. (a) A schematic diagram of the flashing and the stationary equivalent input. (b) Mean DDs of the extended model plotted as a function of flash interval. Green line represents the approximate analytic solution (Eq. (5)), while blue circles represent mean DDs during 1 min in 1 trial of simulation (flash interval = 100 ms, no noise condition). The stimulus strengths of flashing stimuli are set to: L_1 , $L_2 = 0.8$ or 1.0, while those of the stationary equivalent are $L_1 = L_2 = 0.7256$ according to Eq. (6) provided in Supplementary data. In both cases, the system parameters are: $a = a_2 = 2.4$, $g = 3.0$, $\varepsilon = \varepsilon_2 = 0.0$, $M = 1.0$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

discrepancy from the experiment lies in the condition of very small flash intervals (~ 10 ms), which will be considered in Discussion.

We additionally test whether DD is modulated by the flashing input over a wide range of parameter values. The results indicate that the stimulus flashing effect is valid all over the BR phase. The stimulus flashing effect for the flashing input is particularly strong around the upper right or the upper left boundary for fDD or sDD, respectively.

In summary, we introduce a minimal extension to Wilson model that includes stimulus feature dimension. In this model, the flashing stimulus substantially elongates fDD and shortens sDD, which are key characteristics of CFS. In addition, the stimulus flashing effect is enhanced as the flash interval decreases. This effect is observed all over the BR region, and is further enhanced near the borders of the region.

3.4. How stimulus flashing affects dominance duration in the extended model

We consider the mechanisms of CFS in the previous section. For this purpose, an analytic solution for fDD is approximated as Eq. (5). It is derived in the parameter region where normal binocular rivalry takes place (marked light green in Fig. 1). The detailed derivation is found in [Supplementary material](#).

$$T_L = \tau_H \left\{ \ln(g) - \ln \left(\frac{1}{M} + g - (a + a_2) \frac{2 + Mg}{1 + Mg} \frac{L}{R} \right) \right\} \quad (5)$$

The resulting DD derived from this formula is plotted as the green line in Fig. 6b, with the results of simulation (when flash interval is 100 ms) as blue circles. The approximated solution is in good agreement with the simulation result. This solution is comparable to DD in BR, which was obtained in [Wilson \(2007\)](#) as

$$T_L = \tau_H \left\{ \ln(g) - \ln \left(\frac{1}{M} + g - a \frac{L}{R} \right) \right\}.$$

In these equations, the last term in the latter logarithm stands for the contribution of external inputs. One can interpret the reason for the prolongation of DD by flashing stimulus, as the effective increase of input strength from $a \frac{L}{R}$ to $(a + a_2) \frac{2 + Mg}{1 + Mg} \frac{L}{R}$. Note that the equation confirms our observation from simulation that the larger a_2 is, the longer is the DD.

3.5. Dependence of depth of suppression of CFS on the number of units

The extended model examined above is of course too simplified to represent a spatially extended system. To consider more realistic cases, we investigate a model with more than two units. The model is represented as:

$$\tau \frac{dE_{Li}}{dt} = -E_{Li} + M \cdot \max \left(0, L_i(t) - gH_i - \sum_j^N a_i E_{Rj} \right)$$

The equations for H_{Li} and H_{Ri} are identical to those of Eq. (4). For simplicity, we set $a_i = a$ for any i . As in the two-unit model, every unit in this model has different response selectivity. We have considered that the local feature of each flash used in CFS experiment is composed of only one feature (e.g., only 180° of spatial phase instead of the mixture of the 0° and 180°). In this situation the input is applied to only one unit at one time. To model this situation, we adopted the circular stimulation manner, i.e., the flashing input travels over the N units one by one. At a given time, the on-input is thereby applied only to one of the units and the off-inputs are applied to the other units. Note also that the simulation result from this manner gives a conservative estimate of the effect of stimulus flashing compared to other regimes such as on–off switching.

With this model, we investigate the “depth of suppression” associated with BR, FS, and CFS. This topic was psychophysically investigated to elucidate the source of suppression in CFS ([Tsuchiya et al., 2006](#)). First, the effect of the flashing input on DD is measured by the ratio of DD in CFS and DD in BR. We compute the dependence of the ratio on the number of units in the extended model (Fig. 7a). In this figure, the black and gray lines indicate these ratios against the number of units exposed to flashing stimuli and those exposed to stationary stimulus, respectively. As the number of units increases, the former increases while the latter decreases, suggesting that the flashing effect on DD is enhanced.

Subsequently, the depth of suppression of BR, FS and CFS is investigated by simulating the probe detection task, which has been intensively employed to estimate the depth of suppression in BR ([Blake & Camisa, 1979](#); [Fox & Check, 1972](#); [Nguyen, Freeman, & Alais, 2003](#); [Nguyen, Freeman, & Wenderoth, 2001](#); [Norman, Norman, & Bilotta, 2000](#); [Watanabe, Paik, & Blake, 2004](#)). In this task, transient monocular stimulus (“probe”) is briefly superimposed on a rival stimulus. The depth of suppression is estimated as the minimal probe strength that makes the observer visible of it. In our model framework, being visible of stimuli is supposed to correspond to getting dominance of neural activity over units in the opposite eye side. The minimal probe strength that makes a group of neurons get dominance would thereby correspond to the depth of suppression. Fig. 7b shows the dependence of

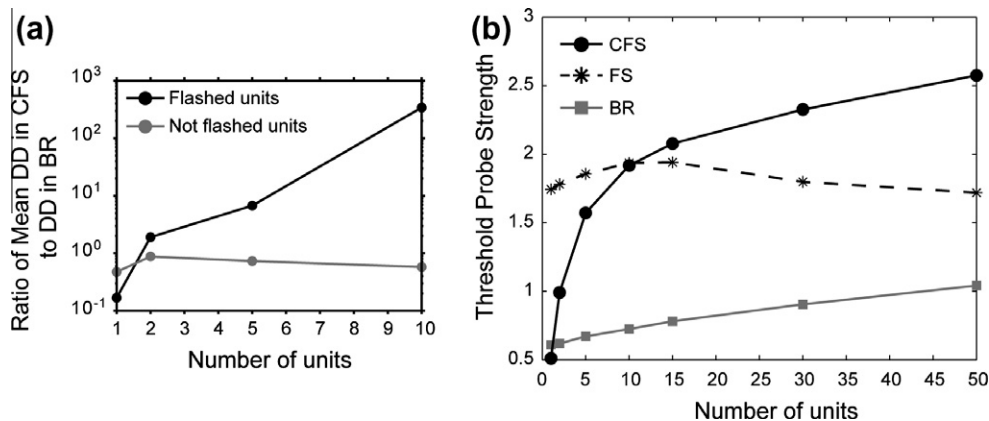


Fig. 7. (a) Ratios of the mean DD in CFS compared to the mean DD in BR, as a function of number of units in the extended model. Flash interval = 100 ms. Black and gray lines indicate the ratios of mean fDD and sDD, respectively. (b) The threshold probe strengths for BR (gray, square), FS (black dot, star) and CFS (black, circle), as a function of the number of units in the extended model. The threshold probe strength was obtained through numerical simulation of probe detection task. The strength of the test stimuli for BR, FS and CFS was held constant to be 1.0 during a trial, while the strength of the probe varied as $probe = \beta + \theta \exp(-t^2/\sigma^2)$, where a baseline stimulus strength $\beta = 0.1$ and standard deviation $\sigma = 100$ ms. During the smooth change of the probe, occurrence of dominance switch is detected. For each probe amplitude, we conduct 100 trials and count the number of the dominance switching from the test stimuli to the probe stimuli. The fraction of the dominance switches consequently produces a sigmoid curve against the probe amplitude. From this curve, we estimate the threshold amplitude at which 50% of trials exhibit dominance switching by applying logistic regression. For the case of FS, the interval between peak time of the probe and the onset of the lagged-stimuli was set to be 150 ms, which was most effective to suppress the probe stimuli. For the case of CFS, the flashing interval was set to be 100 ms in this figure. Simulation with the flash interval of 1.0 ms yielded the basically the same result as 100 ms. $dt = 0.25$ ms. In both cases, the system parameters are: $a_i = 2.4$, $g = 3.0$, $\epsilon = 0.0$, $M = 1.0$ and noise = 5.0×10^{-7} .

threshold probe strength on the number of units. When N is less than 10, the threshold for FS is higher than that for CFS, probably due to differences in timing of the probe. In CFS, after the high, transient response of the flashed units, the units in the opposite eye are stimulated with the probe stimulus. The probe can therefore switch the dominance. On the other hand in FS, the probe comes during the transient response of the flashed unit.

When N is sufficiently large, however, the threshold is highest for CFS, followed by FS and weakest for BR, consistent with the results of the probe detection test by Tsuchiya et al. (2006). Here we qualitatively explain the mechanisms of the phenomena. As explained in the previous paragraph, whether the probe switches the neural dominance depends on amplitude of the transient activity driven by the rival stimulus. The amplitude of the transient response thus gives an approximation of the threshold probe strength. With this approximation, one can get a picture of why the depth of suppression increases in CFS as follows. The transient response is strong when the units are not sufficiently adapted to the external stimuli, i.e., H_s are low. When N is large, each unit receives external input for short period, thereby the unit is less adapted to the external stimuli. This is why threshold probe strength increases with N . When N is increased further, H_s cannot be lower than 0 by definition. Probe strength in CFS therefore saturates at a large N . Next, let us consider the other extreme, when N is less than 10. In CFS, the probe comes when the flashed units are in steady-state after the transient peak response. The probe therefore easily switches the dominance. In FS, however, the probe stimulus comes during the transient response of the flashed unit. This is why probe strength against CFS is smaller than that against FS.

4. Discussion

To understand CFS at a neural circuit level, we studied a model with adaptation and mutual inhibition, revealing that it accounts for the modulation of DD observed in psychophysical experiments of CFS. Other aspects of CFS, such as the effect on afterimage, need further investigation.

One model for CFS was previously proposed by Tsuchiya and Koch (2005), in which both binocular rivalry and flash suppression were considered. Compared to their model, our extended model describes neural circuits underlying CFS explicitly. In addition, our model is based solely on mechanisms of adaptation and inhibition without ad hoc assumptions regarding relationships between stimulus strength and a flash interval.

One may consider CFS results from bottom-up attention elicited by high saliency of the flashing stimuli. Attentional effects have been generally considered to arise from the network with a hierarchical structure. However, the modulation of DD was successfully reproduced in our model without including any hierarchical network architecture. Our findings imply that hierarchical mechanisms are not necessarily required for the modulation of visibility in CFS.

Our results indicate that the effect of the stimulus flashing on DD depends on the strength of the flash. If the flashing stimulus is weaker than the stationary stimulus to the other eye, sDD is markedly shortened by the flashing stimulus. If the flashing stimulus is stronger than the stationary stimulus, however, the flashing stimulus significantly prolongs fDD. Our study thereby suggests that the modulation of DD is easily detected when the stimulus strengths are not balanced between the two eyes.

In exploring the model composed of multiple units, we found that the depth of suppression induced by repetitive flashing is considerably stronger than those by a single flash and stationary stimulus when the number of units is sufficiently large. This strong suppression is probably mediated by maintenance of dominance

without sufficient adaptation of the units. The simulation that investigates the depth of suppression (Fig. 7b) yields results consistent with the psychophysical experiment by Tsuchiya et al. (2006). Using a probe detection task, they measured the suppressive effects of flashing inputs on stimuli given to the other eye, in comparison with those associated with binocular rivalry and flash suppression, and found that the threshold contrast for CFS is much higher than those for FS and BR.

Although our model accounts for the principal features of CFS, a discrepancy still remains between the model and psychophysical experiments. In the experiment by Tsuchiya and Koch (2005), stimulus flashing at extremely high frequencies no longer suppressed the stationary stimulus. Specifically, the DD for extremely short flash intervals (~ 10 ms) were nearly equal to those associated with a stationary stimulus (see Fig. 3a, leftmost points). In our model, however, the fDD is larger than the sDD for extremely short flash intervals. Our study modeled only groups of neurons in cortex where neural rivalry takes place. However, when a pathway to the cortex is considered, it is probable that external stimuli of high-frequency do not reach the cortex. Therefore, increasing flash frequency probably decreases neural excitability, resulting in a decrease in DD. Some physiological studies of cat and monkey LGN and early visual cortex (Hamilton, Albrecht, & Geisler, 1989; Hawken, Shapley, & Grosf, 1996; Movshon, Thompson, & Tolhurst, 1978) support this picture. In these studies, majority of examined neurons exhibited high-frequency cut-off. In addition, the cut-off frequency decreased when the recording cortical area was far from the retina.

The possibility of extending models for BR to stimulus feature space has been proposed elsewhere. For example, Freeman (2005) proposed a model with four parallel visual channels, two driven by the left eye and the others by the right, to account for the timing of dominance intervals in distributed neural processing in rivalry. Unlike this study, our purpose here was to determine the essential requirements for accounting for CFS. Our study demonstrates the importance of including stimulus feature space in examination of CFS for the first time.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.visres.2011.01.009](https://doi.org/10.1016/j.visres.2011.01.009).

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