Stochastic resonance in binocular rivalry

Yee-Joon Kim, Marcia Grabowecky, Satoru Suzuki *

Department of Psychology, Institute for Neuroscience, Northwestern University, Evanston, IL 60208, USA

Abstract

When a different image is presented to each eye, visual awareness spontaneously alternates between the two images—a phenomenon called binocular rivalry. Because binocular rivalry is characterized by two marginally stable perceptual states and spontaneous, apparently stochastic, switching between them, it has been speculated that switches in perceptual awareness reflect a double-well-potential type computational architecture coupled with noise. To characterize this noise-mediated mechanism, we investigated whether stimulus input, neural adaptation, and inhibitory modulations (thought to underlie perceptual switches) interacted with noise in such a way that the system produced stochastic resonance. By subjecting binocular rivalry to weak periodic contrast modulations spanning a range of frequencies, we demonstrated quantitative evidence of stochastic resonance in binocular rivalry. Our behavioral results combined with computational simulations provided insights into the nature of the internal noise (its magnitude, locus, and calibration) that is relevant to perceptual switching, as well as provided novel dynamic constraints on computational models designed to capture the neural mechanisms underlying perceptual switching.
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1. Introduction

Making flexible decisions requires consideration of multiple potential interpretations of a given situation. It is therefore crucial to maintain conscious awareness in a meta-stable state in which each state of awareness is only marginally stable, such that awareness can shift among multiple interpretations compatible with a given stimulus environment. In the visual domain, this translates to dynamic perceptual switching among alternative scene interpretations, for example, seeing "the trees within the forest" and "the forest made up of the trees." This flexibility is important because behaviorally significant information may exist at different levels of scene organization (e.g., a tiger hidden behind a tree, a layout

of the trees indicating a path; see Leopold & Logothetis, 1999 for a discussion of the functional significance of perceptual multistability).

A classic psychophysical paradigm used to study spontaneous perceptual switching is binocular rivalry. When a different image is presented to each eye using a stereoscope, the perceived image, rather than being a superposition of the two images, tends to spontaneously alternate between them, typically every 0.5–3 s (e.g., Blake, 1989; Blake, 2001; Blake & Logothetis, 2002; Logothetis, 1998). Binocular rivalry can also be multistable (involving more than two interpretations; e.g., Suzuki & Grabowecky, 2002a). The observer typically views a rivalrous display continuously, and presses a key corresponding to the visible (dominant) image whenever the percept switches. Data from binocular rivalry thus typically consist of a time series of perceptual-dominance durations for the two competing images. Because the physical stimuli remain constant during

* Corresponding author. Tel.: +1 847 467 1271; fax: +1 847 491 7859.
E-mail address: satoru@northwestern.edu (S. Suzuki).

binocular rivalry and the dynamics of rivalry are similar whether or not images are stabilized on the retina (e.g., Blake, Fox, & McIntyre, 1971; Wade, 1974), perceptual alternations during binocular rivalry reveal brain mechanisms involved in controlling states of visual awareness.

Spontaneous perceptual alternations in binocular rivalry are thought to result from adaptation and inhibitory interactions occurring at multiple processing stages involving neural populations responsive to different aspects of the competing images. For example, behavioral studies have provided evidence for both eye-based competition (presumably mediated by monocular neurons in V1[1]; e.g., Blake & Fox, 1974; Blake, Westendorf, & Overton, 1980; Lack, 1974; Lee & Blake, 1999) and pattern-based competition (presumably mediated by binocular neurons in higher visual areas; e.g., Logothetis, Leopold, & Sheinberg, 1996). Human brain imaging (fMRI) studies suggest a prominent role of V1 and/or a prominent role of feedback signals to V1 from higher visual areas (e.g., Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001) in resolving perceptual competition. Primate single-cell recording studies (measuring spike rates) found that all-or-none type competition did not occur until inferotemporal cortex while the lower visual areas played intermediate roles (e.g., Leopold & Logothetis, 1996; Logothetis, 1998; Sheinberg & Logothetis, 1997). Electrophysiological studies (e.g., EEG and MEG) have suggested that overall neural activity was stronger and more coherent for a visible image than for a suppressed image during binocular rivalry (e.g., Brown & Norcia, 1997; Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Russell, & Edelman, 1998). A full understanding of the intricate multi-stage neural interactions underlying perceptual switching requires a deeper understanding of how neural population activity measured by fMRI, EEG, and MEG are related to single-cell activity (e.g., Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993; Logothetis, 2003; Vanni et al., 2004).

To tackle perceptual multistability from an implementation perspective, computational models of binocular rivalry have focused on simplified systems that can account for behavioral results to date, aiming to understand the core mechanisms underlying spontaneous perceptual switching. These "macroscopic" models typically involve inhibitory interactions between two pools of neural units preferentially tuned to the competing images (e.g., Blake, 1989; Lehky, 1988; Sugie, 1982; Wilson, 1999). Appropriate implementations of non-linearity in these inhibitory interactions (potentially medi-

ated by spike-frequency adaptation and synaptic depression; e.g., Laing & Chow, 2002) allow a model system to exhibit the mutually exclusive, all-or-none, perceptual switches typically observed in binocular rivalry (e.g., Wilson, 1999). The existing models are successful in generating spontaneous oscillatory behavior and in simulating time-averaged behaviors of binocular rivalry such as how average dominance durations of the competing images depend on their absolute and relative luminance contrasts (e.g., Laing & Chow, 2002; Lehky, 1988; Mueller, 1990; Wilson, 2003). However, these models have not been rigorously tested with respect to their dynamics.

Binocular rivalry as well as other forms of perceptual multistability (e.g., monocular rivalry and figural multistability; see Leopold & Logothetis, 1999 and Blake & Logothetis, 2002 for reviews) exhibit stochastic dynamics; that is, though the time series of perceptual alternations tend to be roughly periodic, the current duration of perceptual dominance cannot be predicted on the basis of the prior dynamics of dominance durations (e.g., lack of autocorrelation, Lathrop values not significantly different from 1, and no evidence of deterministic chaos; e.g.,Blake et al., 1971; Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972; Fox & Herrmann, 1967; Lathrop, 1966; Lehky, 1995; Richards, Wilson, & Sommer, 1994; Taylor & Aldridge, 1974). Because of these stochastic dynamics, it has been speculated that internal neural noise (in addition to adaptation and inhibitory neural interactions) might play a crucial role in initiating spontaneous perceptual switches (e.g., Blake, 2001; Haken, 1995; Lehky, 1988; Sugie, 1982). Accordingly, random noise was typically added to the activity of the simulated neural units. The dynamic behaviors of the models were then verified by successful fits of the positively skewed frequency distributions of dominance durations obtained from spontaneous binocular rivalry (e.g., Laing & Chow, 2002; Lehky, 1988; Wilson, 1999).

The shapes of spontaneous dominance-duration distributions, however, do not provide adequately rigorous constraints for testing model dynamics; any model that has adaptation, inhibitory interactions, and noise as free parameters can generate appropriately positively skewed dominance-duration distributions. Thus, there is a need for new empirical constraints on the dynamics of binocular rivalry to both distinguish among and improve existing models. Furthermore, despite the hypothesized role of internal noise in initiating perceptual switches, there has been little evaluation of the nature of this internal neural noise. We thus actively probed the dynamics of perceptual switches using a perturbation technique to determine whether the underlying neural adaptation and inhibitory interactions were coupled with noise in such a way that the system produced stochastic resonance. As we will discuss later, a demonstration of stochastic resonance in binocular rivalry

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[1] Eye preferences are also preserved to some degree in higher cortical visual areas (e.g., Gross, Rocha-Miranda, & Bender, 1972; see the discussion section of Schröder, Fries, Roelfsema, Singer, & Engel, 2002 for a brief review).

provides novel dynamic constraints on the existing and future computational models of spontaneous perceptual switching.

The two most prominent features of binocular rivalry, (1) mutually exclusive (non-linear) perceptual switches and (2) the stochastic nature of the time series of the dominance durations, are compatible with a double-well potential framework (e.g., Gammaitoni, Hanggi, Jung, & Marchesoni, 1998; Haken, 1995; Suzuki & Grabowecky, 2002a; see Sperling, 1970, for an early theoretical application of a double-well potential framework to the dynamics of binocular fusion, stereopsis, and rivalry). In this framework, the two potential wells correspond to the two alternating, marginally stable percepts. Intuitively, the perceptual state can be considered to be like a ball (depicted with a smiley-face in Fig. 1) that temporarily gets trapped in one of the two wells. The ball jitters due to random noise, and when the amplitude of the jitter happens to exceed the potential barrier between the two wells, the ball hops to the other well and the percept switches. Thus, greater noise (relative to the height of the potential barrier) should on average produce faster perceptual switches. In addition, neural adaptation and
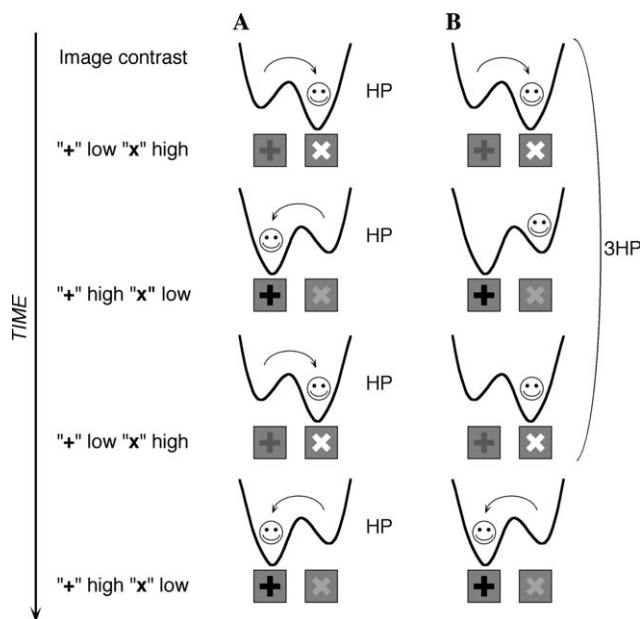

Fig. 1. A cartoon illustration of a double-well potential framework describing binocular rivalry under periodic contrast modulations. The left and right wells correspond to representations of the "+" and "x" shapes, respectively. The depths of the two wells were periodically modulated in opposite phase by modulating the luminance contrasts of the two images in opposite phase (see text for details). The position of the smiley face represents the perceptual state (i.e., the perceived shape). If the neural mechanisms underlying the double-well potential landscape interacted appropriately with noise to produce stochastic resonance under appropriate conditions, the dominance-duration distribution should show resonance peaks at (A) one times the contrast-modulation half-period, *HP*, (B) three times the modulation half-period, 3 *HP*, and at other odd-integer multiples of the modulation half-period.

inhibitory interactions could raise the well that has the ball, making the ball more likely to hop to the other well. Thus, stronger adaptation and inhibitory interactions could also increase the switching rate.

All dynamic models of binocular rivalry are overall consistent with a double-well potential framework by virtue of successfully generating two marginally stable states (e.g., Wilson, 1999). However, if the switching between the marginally stable states were generated by a particular type of coupling between neural interactions and noise, spontaneous alternations between the two states could be probabilistically influenced by an applied periodic perturbation that modulates the strengths of the two states (i.e., the depth of the two wells) in opposite phase. Specifically, a resonance should occur when the frequency of the periodic signal matches the average spontaneous alternation rate of the system (see Gammaitoni et al., 1998, for mathematical derivations). This phenomenon is generally known as stochastic resonance—a noise-mediated cooperative phenomenon in which noise increases sensitivity to a weak periodic signal when the frequency of the periodic signal matches the intrinsic noise-dependent time-scale of the system (e.g., Bulsara, Jacobs, Zhou, Moss, & Kiss, 1991; Gammaitoni et al., 1998; Longtin, Bulsara, & Moss, 1991; Wiesenfeld & Moss, 1995).

To determine whether the mechanisms underlying binocular rivalry supported stochastic resonance, we perturbed the relative strength of the two perceptual states by modulating the luminance contrast of the competing stimuli in opposite phase. It is known that the dominance duration is on average longer for the image with higher luminance contrast when other factors such as motion, contour density, and grouping are held constant (see Blake & Logothetis, 2002, for a review). Specifically, increasing and decreasing the contrast of one image primarily decreases and increases, respectively, the dominance duration of the competing image (Levelt's 2nd proposition, Levelt, 1965). A longer dominance duration implies a deeper potential well because it takes longer for the perceptual state to hop out of a deeper well than out of a shallower well. Thus, increasing and decreasing the contrast of one image should make the potential well for the competing image shallower and deeper, respectively. Because we varied the contrast of the competing images simultaneously in opposite phase, the depth of the two potential wells should have been modulated in opposite phase. Thus, if adaptation, inhibitory modulations, and noise underlying binocular rivalry interacted in a specific way that satisfied the requirements for stochastic resonance, rivalry should be maximally influenced by a periodic contrast modulation when the modulation frequency matches the average spontaneous rate of perceptual switching.

In previous studies in which stochastic resonance was induced in biological systems (the central and peripheral

nervous systems of paddlefish, crayfish, crickets, and humans), an appropriate level of external noise was added to adjust the system's dynamics to match the specific frequency of a weak periodic signal (e.g., Cordo et al., 1997; Douglass, Wilkens, Pantazelou, & Moss, 1993; Levin & Miller, 1996; Mori & Kai, 2002; Russell, Wilkens, & Moss, 1999; Simonotto et al., 1997). Theoretically, internal noise should be just as effective as external noise in producing stochastic resonance (e.g., Gluckman et al., 1996; Hänggi, 2002; Riani & Simonotto, 1994). In particular, Riani and Simonotto (1994) reported computer simulation results predicting that the internal neural noise in an appropriate double-well-potential framework could support both spontaneous perceptual switching and stochastic resonance in perception of ambiguous figures. We tested this prediction by attempting to induce internal-noise-based stochastic resonance in the human visual system for mechanisms that control spontaneous perceptual switches in binocular rivalry.

In attempting to induce stochastic resonance in perceptual switching, it is technically difficult to systematically vary the magnitude of the relevant internal neural noise. For example, rapidly and randomly fluctuating the image contrast would not generate corresponding neural noise at the processing stages critical to perceptual switching because binocular rivalry exhibits a wide (several hundred milliseconds) window of temporal summation (O'Shea & Crassini, 1984). Thus, instead of varying the internal noise to adjust the dynamics of spontaneous perceptual switching to match the frequency of a periodic signal, we varied the frequency of a periodic signal to attempt to match the existing internal-noise-based dynamics of perceptual switching.

We first induced clear spontaneous perceptual alternations between a "+" shape and an "x" shape by projecting them to different eyes (using a stereoscope). We then applied periodic signals by modulating the luminance contrasts of the two shapes in opposite phase (i.e., when one shape was higher contrast, the other shape was lower contrast). This hypothetically corresponds to modulating the depths of the two potential wells, one corresponding to the percept of "+" and the other corresponding to the percept of "x," in opposite phase (see Fig. 1 and the discussion above). We then predicted that binocular rivalry should exhibit stochastic resonance when the contrast-modulation frequency matched the average rate of spontaneous perceptual switching.

It is important to note that the amplitude of contrast modulation must be appropriately tuned to the magnitude of the internal noise (e.g., Ward, 2002). On the one hand, when the modulation amplitude is substantially lower than the internal noise, the signal is too weak to influence binocular rivalry because perceptual alternations will be predominantly influenced by inter-

nal noise; on the other hand, when the modulation amplitude is substantially higher than the internal noise, binocular rivalry will be completely captured by the contrast modulation (e.g., O'Shea & Crassini, 1984). Note that a signal that is too weak to modulate perceptual switching may still be clearly visible (i.e., above sensory threshold). The requirement that the contrast-modulation amplitude must be appropriately tuned to the magnitude of the internal noise for induction of stochastic resonance provides a method to probe the internal noise that influences the dynamics of perceptual switching. Specifically, by finding an appropriate amplitude of contrast modulation that induces stochastic resonance in binocular rivalry, we can estimate the magnitude of the relevant internal noise in terms of the equivalent contrast-modulation amplitude.

If the mechanisms underlying binocular rivalry support stochastic resonance, in addition to the strong resonance that occurs when the signal frequency matches the spontaneous rate of perceptual alternation, higher-order resonance peaks should be observed (when modulation frequencies are appropriate) in the dominance-duration distributions at the odd-integer multiples of the half-period of contrast modulation. Although the reader is referred to Gammaitoni et al. (1998) for the mathematical derivations, we present the following intuitive description. In our cartoon illustration of an appropriate double-well potential framework shown in Fig. 1, the noise is coupled linearly with the periodic signal; in other words, while the depths of the two potential wells oscillate in opposite phase (due to the periodic signal), the noise adds random jitter that probabilistically tosses the state across the middle barrier. The primary peak of the dominance duration distribution should occur exactly at the modulation half-period as a consequence of a tendency for the perceptual state (i.e., the perceived shape) to change in synchrony with the oscillation of the wells (i.e., the changes in the relative contrast of the two shapes) (Fig. 1A). This primary peak should become predominant at resonance when the contrast-modulation half-period matches the average dominance duration of spontaneous perceptual switching. A second peak (if any) should occur at three times the modulation half-period when perception fails to shift at the first favorable change in the relative contrast, and shifts at the next favorable change (Fig. 1B). Similarly, a third peak should occur at five times the modulation half-period when perception fails to shift at two consecutive favorable changes in contrast, and so on. The higher order peaks should occur with diminishing gains.

To summarize, if the mechanisms underlying perceptual alternations in binocular rivalry are characterized by a particular type of double-well potential landscape and noise that supports stochastic resonance, the relevant differential equations make the following quantitative predictions. When binocular rivalry is subjected to

contrast modulation of an amplitude tuned to the magnitude of internal noise (1) a resonance should occur when the frequency of contrast modulation matches the average spontaneous alternation rate of binocular rivalry, and (2) dominance-duration distributions should exhibit peaks at the odd-integer multiples of the half-period of contrast modulation. By psychophysically demonstrating these predicted phenomena, we revealed internal-noise-based stochastic resonance in perceptual switching, and provided insights into the nature of the relevant internal noise (its magnitude, locus, and calibration). Furthermore, by evaluating how some representative dynamic models of binocular rivalry are constrained by the current results, we demonstrated the importance and usefulness of the requirement of stochastic resonance in modeling perceptual switching.

2. Methods

2.1. Observers

Two psychophysically trained observers, YS and ET, who were naïve to the purpose of the experiments, and author SS, participated.

2.2. Stimuli and procedure

A dark "+" shape and a light "x" shape were used as rivaling patterns (see Fig. 2). They were presented against a gray immediate background (70 cd/m^2 in the blink-allowed condition [YS only] or 46 cd/m^2 in the no-blink condition [all observers]) on a 21 in. color monitor (75 Hz) in a dimly lit room, using Vision Shell software (Micro ML). A stereoscope consisting of four front-surface mirrors and a central divider was used to present stimuli dichoptically. To facilitate exclusive binocular rivalry (i.e., clear alternations of "+" and "x" without perception of mixed parts from both shapes), the rivaling patterns were small (<1° visual angle), opposite in luminance polarity, consisted of differentially oriented edges, and were presented parafoveally (∼0.35° eccentricity).

All observers were tested in the no-blink condition (no blinking allowed during each continuous stimulus observation). YS was also tested in the blink-allowed condition (natural blinking) to verify that the pattern of results was not influenced by blinking. All the results discussed were equivalent whether or not blinking was allowed.

In each trial in the blink-allowed condition, YS continuously viewed the rivalry display for 60 s while indicating, by pressing joystick buttons, the perceived shape ("+" or "x") whenever it changed; in no case were perceptual alternations too rapid to be reported with manual button presses. In the no-blink condition (all observers), each 60 s run was replaced by a pair of

16 s runs with a short break in between; trials in which blinking occurred were replaced.

The luminance contrasts of the two shapes were square-wave[2] modulated in opposite phase (i.e., when one shape was higher contrast, the other shape was lower contrast). We defined the higher contrast as the *baseline contrast* because the amplitude of the contrast modulation was always varied by choosing a different value for the lower contrast; we used the usual definition of image contrast, $C = \frac{L_{\text{Stimulus}} - L_{\text{Background}}}{L_{\text{Stimulus}} + L_{\text{Background}}}$, where L indicates luminance.

In the blink-allowed condition (YS only), the baseline contrast, C_{Baseline}, was always 0.50. The lower contrast, C_{Lower}, was chosen such that the percent contrast modulation, defined as $\frac{C_{\text{Baseline}} - C_{\text{Lower}}}{C_{\text{Baseline}}} \times 100\%$, was either 40% or 20%.

In the no-blink condition (all observers), two baseline contrasts, $C_{\text{Baseline}} = 0.50$ and $C_{\text{Baseline}} = 0.25$, were used to test the possibility that the influence of contrast modulation on binocular rivalry might depend on the percent contrast modulation independently of the baseline contrast. For each baseline contrast, the percent contrast modulation was either 30% (tested for all observers) or 20% (tested for SS and YS).

Due to normal monitor drift over time, the contrasts slightly varied across sessions ($SD = 0.004$). The contrast-modulation frequency was constant during each trial.

Each experimental session consisted of a sweep of contrast-modulation frequencies from 0.28 to 2.48 Hz. The frequencies were varied either in the ascending or descending order while the baseline contrast and the

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[2] We used square-wave rather than sinusoidal contrast modulations partly to keep the impacts of the rising and falling components of the contrast signals constant across different modulation frequencies. Higher harmonics in the square-wave (i.e., 3rd, 5th, 7th,...) could have produced multiple primary resonances at 3, 5, 7,..., times faster than the modulation frequency. These resonances could have shown up in the dominance duration distributions as peaks faster than the primary peak for the fundamental frequency. Such peaks were not evident in the data (see Fig. 3) presumably because the amplitudes of the higher harmonics (falling by $1/k$ for the kth harmonic) would have been too small to generate detectable resonance. Furthermore, the higher harmonics would have been irrelevant when the modulation half-period was 600 ms or faster because even the 3rd harmonic would have had the half-period of 200 ms or shorter. This would have been too fast to exert any influence because even when the fundamental had the half-period of 200 ms, no corresponding peak occurred (see the lack of resonance peak corresponding to the modulation half-period, HP, in the rightmost dominance-duration distribution shown in Fig. 3). This is important because we obtained evidence of odd-integer multiple peaks in the dominance-duration distributions most strongly for half-periods of 400 and 600 ms, for which the higher harmonics of the square-waves would have made no contributions. Finally, we note that a transient signal presented to one eye can induce dominance of the corresponding stimulus (e.g., Wolfe, 1984). In our design, such transient effects were cancelled out because the contrasts in the two eyes were simultaneously modulated.
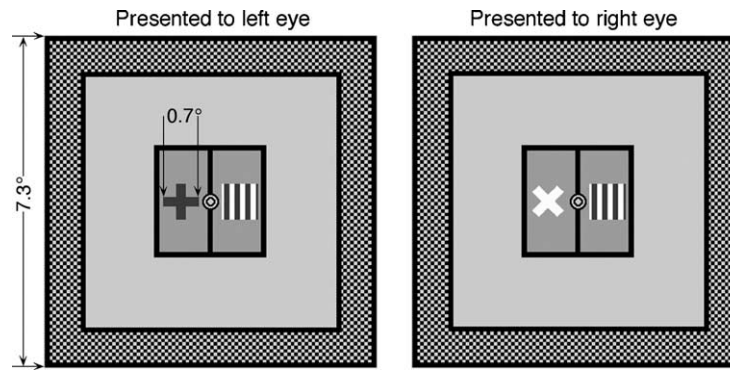
Fig. 2. The stimuli used to induce binocular rivalry. The two images were presented dichoptically using a four-mirror stereoscope. The high-contrast textured frames were binocularly presented around the rivaling shapes to facilitate stable binocular alignment. Perception spontaneously alternated between "+" and "x" shapes. To induce stochastic resonance, the luminance contrasts of the two shapes were temporally modulated in opposite phase at various frequencies. A non-rivaling grating was presented binocularly on the right side (as shown in the figure) to balance the overall stimulus configuration and help stabilize fixation (the grating was not presented in the blink-allowed condition).

amplitude of contrast modulation remained constant. The order of modulation frequency (ascending or descending), the amplitude of modulation, and the baseline contrast were counterbalanced across sessions.

Control data were collected at the beginning and end of each session. In these control trials, the contrast was modulated more slowly than the maximum spontaneous dominance duration (using a half-period = 6 s for the blink-allowed and a half-period = 8 s for the no-blink conditions). This procedure was used to measure spontaneous alternation rates while the static image contrasts were matched to the experimental conditions in which contrast-modulation frequencies were varied within the range of spontaneous alternation rates. At least a 2-min break was given between trials, and each session lasted 1–2 h (typically, not more than one session per day). The 2-min breaks were sufficient to allow the visual system to recover from contrast adaptation from each trial (e.g., Suzuki & Grabowecky, 2004).

Observer YS completed 20 sessions (in 47 days) of the blink-allowed condition (yielding an average number of perceptual alternations, $\bar{N} = 453$, for each combination of contrast-modulation frequency, modulation amplitude, and baseline contrast) and 32 sessions (in 139 days) of the no-blink condition ($\bar{N} = 182$); SS completed 32 sessions (in 83 days) of the no-blink condition ($\bar{N} = 246$); ET completed 16 sessions (in 80 days) of the no-blink condition ($\bar{N} = 213$). The $\bar{N}$ for YS in the blink-allowed condition was large because of the longer viewing time per trial and the larger number of trials.

3. Results

Each graph in the lower half of Fig. 3 shows the dominance-duration distribution when binocular rivalry was subjected to contrast modulation at a given frequency (indicated at the top of Fig. 3). The data have been averaged across the three observers and the 0.50 and 0.25 baseline contrasts. All characteristics of the data discussed below were present in the individual cases except that the distributions were noisier due to the smaller number of data points. The contrast-modulation amplitude was 30–40% of the baseline contrasts, which was within an appropriate range to induce stochastic resonance (a 20% modulation was ineffective; see Figs. 4 and 5).

The leftmost graph shows the spontaneous (control) dominance-duration distribution in the absence of an effective contrast modulation. In the graphs to the right, the dominance-duration distributions are shown for increasing contrast-modulation frequencies. In each graph, the odd-integer multiples of the modulation half-period are indicated by the vertical lines.

It is clear that the peaks in the dominance-duration distributions occurred at the odd-integer multiples of the half-period of contrast modulation. When the contrast modulation was slow (0.28–0.31 Hz), only the primary peak at the modulation half-period was evident and the peak was small. The primary peak grew in size as the modulation frequency was increased toward resonance (at about 0.50 Hz; see Figs. 3 and 5). As the modulation frequency was increased beyond the primary resonance frequency, higher-order peaks began to appear at the odd-integer multiples of the modulation half-period (see 0.63–2.48 Hz modulations). In the upper graphs in Fig. 3, the leftmost control distribution, reflecting spontaneous perceptual alternations, has been subtracted from each distribution to more clearly show the peaks attributable to the periodic contrast modulations.

Note that when the contrast-modulation frequency was 2.48 Hz (the rightmost graph in Fig. 3), the primary peak at the modulation half-period was missing and the first peak was at three times the modulation half-period.
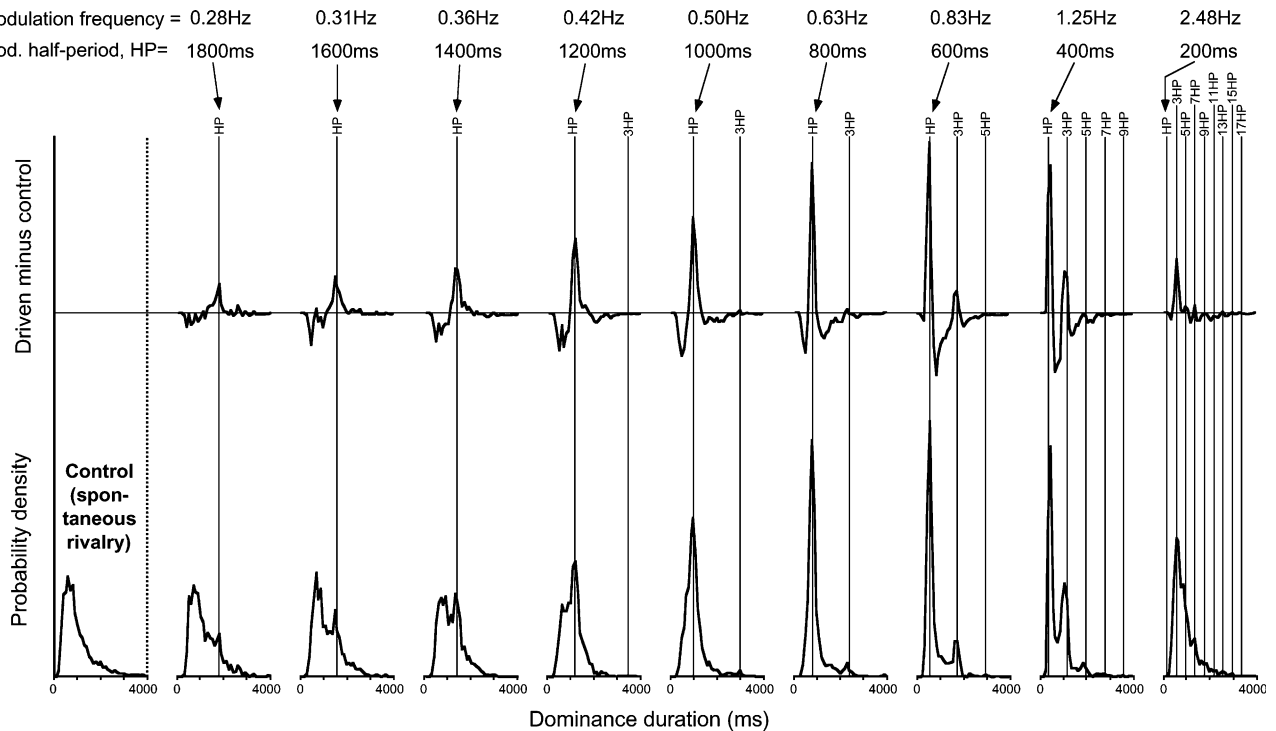
Fig. 3. Distributions of perceptual dominance duration in binocular rivalry when the contrasts of the competing images were modulated in opposite phase at frequencies of 0.28–2.48 Hz (with the corresponding half-periods [HP] of 1800–200 ms). The distributions have been averaged for the three observers, the 0.50 and 0.25 baseline contrasts, and the blink-allowed and no-blink conditions (the overall patterns were similar when each condition from each observer was examined separately). The bottom graphs show peaks in the dominance-duration distributions at the odd-integer multiples of the contrast-modulation half-period (indicated by the vertical lines), consistent with the presence of stochastic resonance. In the top graphs, the control distribution has been subtracted to isolate gains due to the periodic contrast-modulation signal.

Interestingly, the 2.48 Hz contrast modulation was clearly visible, and attention mechanisms are known to track much faster stimulus alternations, up to 4 Hz or even 10 Hz (see Suzuki & Grabowecky, 2002b, for a review). The absence of the primary peak at 2.48 Hz thus suggests that the mechanisms underlying perceptual alternations in binocular rivalry have their own slow time constraints.

The odd-integer multiple peaks characteristic of stochastic resonance were clearly demonstrated in perceptual alternations in binocular rivalry. We next examined the other signature of stochastic resonance, that maximum resonance (i.e., the maximum influence of contrast modulation) should occur when the contrast-modulation frequency matches the average spontaneous rate of perceptual switching. We first examined intuitive evidence of resonance on the basis of a non-monotonic gain as a function of the modulation frequency. We then verified that the resonance frequency followed variations in the average spontaneous alternation rate.

The influence of each contrast-modulation frequency on perceptual switching can be indexed by the size of the induced primary peak in the dominance-duration distribution at the modulation half-period, which is called P_1 (Gammaitoni, Marchesoni, Menichiella-Saetta, & Santuci, 1989; Gammaitoni et al., 1998). Typical-

ly, P_1 is defined as the proportion of the area under the dominance-duration distribution curve within the range of $HP \pm HP/2$, where HP indicates the modulation half-period. P_1 is plotted as a function of the contrast-modulation frequency for the three observers in the upper panels of Fig. 4 (solid curves). Because the dominance-duration distributions were peaked even without contrast modulation (see the leftmost graph in Fig. 3), the corresponding proportions of area of the control distribution (dashed curves) must be subtracted to obtain the gain in P_1 attributable to the periodic contrast modulations (e.g., Giacomelli, Marin, & Rabbiaosi, 1999). This P_1 gain (the solid curve minus the dashed curve) is shown in the lower panels of Fig. 4 as a function of the contrast-modulation frequency. For the 30% and 40% contrast modulations (the primary graphs in Fig. 4), the presence of resonance is clearly indicated by the fact that the P_1 gain functions were non-monotonic and strongly peaked (e.g., Gammaitoni, Marchesoni, & Santuci, 1995). In contrast, the evidence of resonance was much reduced (or absent) when the modulation amplitude was 20% (see the inset graphs in Figs. 4A and B, showing nearly overlapping P_1 and control functions in the upper panels, and the flattened P_1 gain functions in the lower panels).
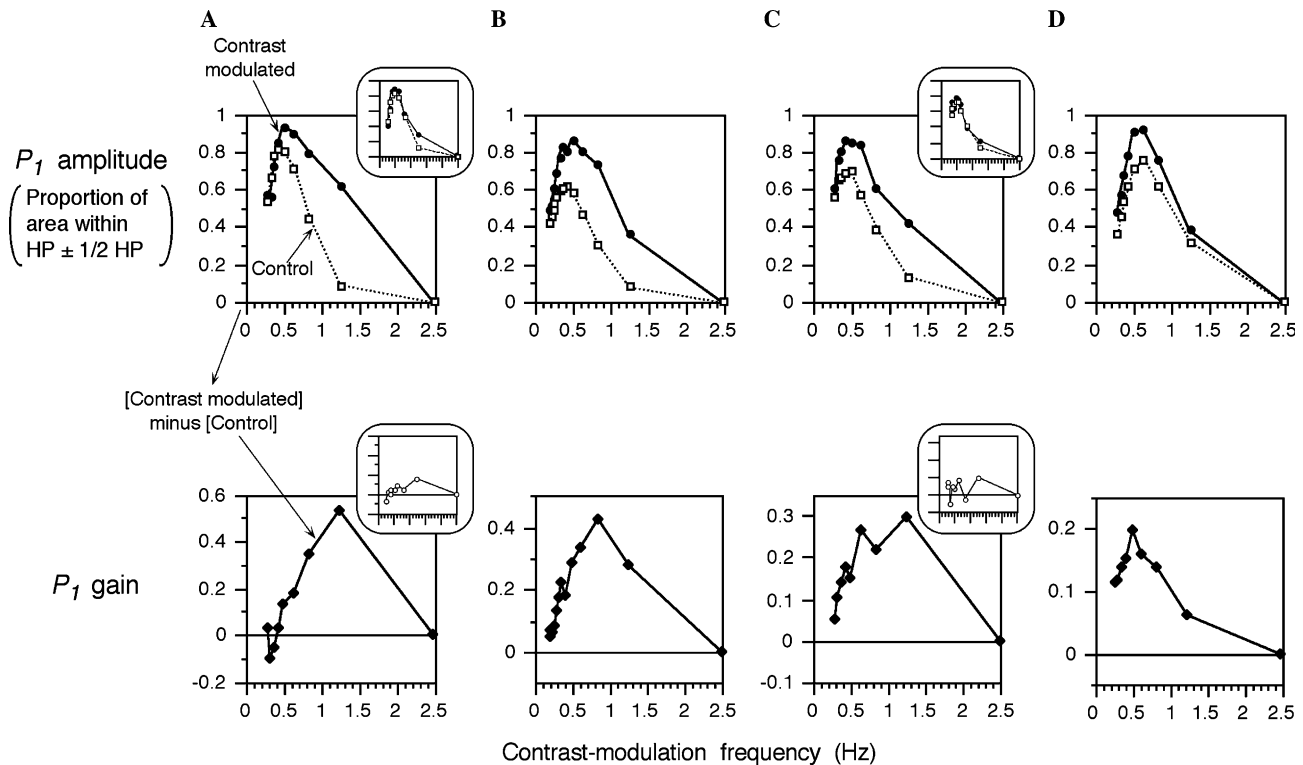
Fig. 4. P_1 amplitude and gain due to periodic contrast-modulation signals. Upper panels: P_1 amplitude for the dominance-duration distributions as a function of the contrast-modulation frequency (solid curve), and the corresponding area proportions for the control distributions (dashed curve). Lower panels: P_1 gain computed as the difference between the solid and dashed curves from the upper panels. (A) Observer SS, 0.25 baseline contrast with no blinking. (B) Observer YS, 0.50 baseline contrast with blinking allowed. (C) Observer YS, 0.50 baseline contrast with no blinking. (D) Observer ET, 0.50 baseline contrast with no blinking. The primary graphs show the results with contrast-modulation amplitudes of 30% (A, C, and D) and 40% (B). The inset graphs (A and C) show the results with 20% contrast modulations. For all observers, the results with other baseline contrasts were similar.

Non-monotonic (i.e., peaked) P_1 and P_1 gain functions are intuitively appealing for revealing the presence of resonance. However, they may not be appropriate for estimating resonance frequencies (e.g., Choi, Fox, & Jung, 1998). This is partly because P_1 functions and the corresponding control functions peak at similar frequencies (upper panels of Fig. 4). The peak of a P_1 function might thus be primarily due to the peak of the corresponding control function, and the peak of a P_1 gain function is likely to be distorted around the peak of the control function due to ceiling effects (note $P_1 \leqslant 1$).

To circumvent this problem in estimating the resonance frequency, we used the coefficient of variation (CV), a typically used index of resonance, which is the ratio of the standard deviation to the mean of a dominance-duration distribution (e.g., Pikovsky & Kurths, 1997). This index, also known as the noise-to-signal ratio, is commonly used in neurophysiology to quantify the regularity of neural responses. CV is defined independently of the shape of a time-interval distribution, and has been applied to positively skewed distributions such as ours (e.g., Dayan & Abbott, 2001; Gabbiani & Koch, 1999; Koch, 1999). CV is particularly useful in

cases such as ours where the magnitude of the internal noise is unknown (note that computation of the signal-to-noise ratio, SNR, for example, requires knowledge of both the noise magnitude and the signal amplitude). Because a lower CV indicates greater periodicity, resonance is indicated by a sharp dip in the CV value[3] as a function of the contrast-modulation frequency (Fig. 5). The modulation frequency corresponding to the bottom of the dip is the resonance frequency. As can be seen in Fig. 5, the resonance frequency approximately matched the average spontaneous alternation rate (indicated by the vertical gray bands in Fig. 5) for all observers and for both 0.50 and 0.25 baseline contrasts. The CV resonance dips were evident when the contrast-modulation amplitude was 30% (the primary graphs in Fig. 5), but

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[3] Means and standard deviations of perceptual-dominance durations are substantially affected by the rare occurrences of unusually slow dominance durations. Thus, for each contrast-modulation frequency and baseline contrast for each observer, dominance durations over three standard deviations from the respective means were excluded when computing the CV. This resulted in exclusion of less than 2% of the data. Note that the conclusions drawn from the data remain the same even when the longer durations are de-emphasized using a log transform rather than trimming outliers.
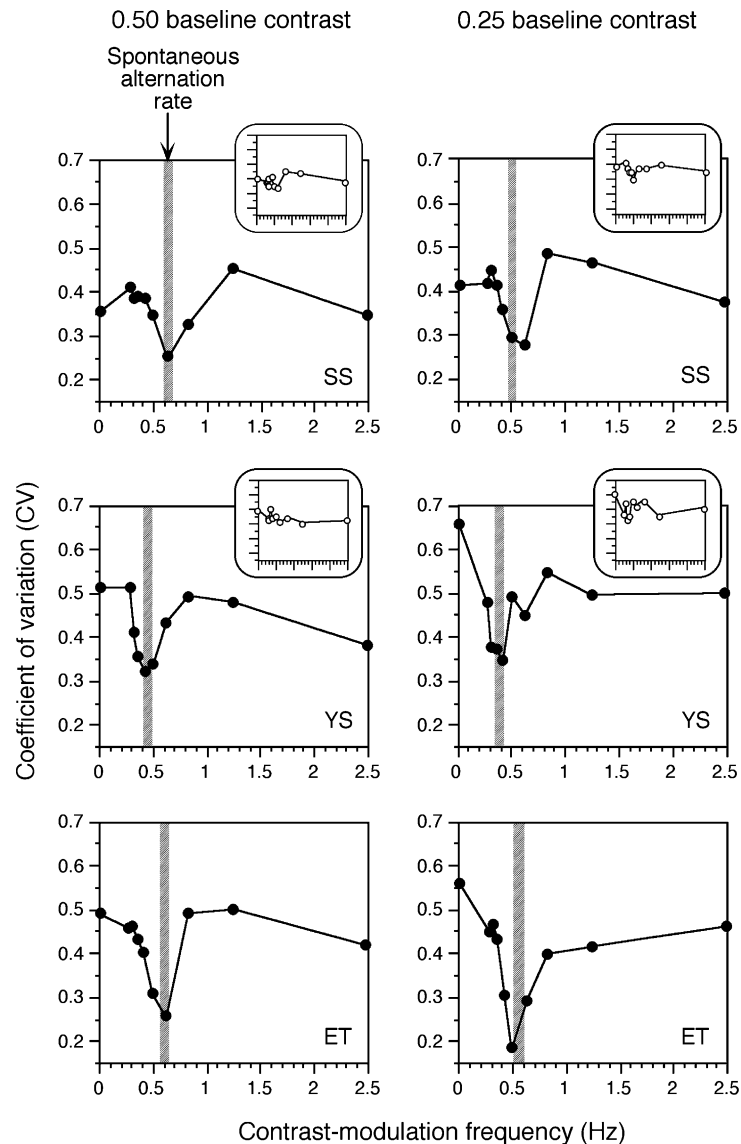
Fig. 5. Coefficient of variation (CV = standard deviation/mean) as a function of the contrast-modulation frequency (Hz). The data (the no-blink conditions only) are shown for the baseline contrasts of 0.50 (left panels) and 0.25 (right panels) for each observer. The gray bands represent the average spontaneous alternation rates (the lower and upper bounds derived from the mean and median dominance durations, respectively). The primary graphs show the results with 30% contrast modulations. The inset graphs (for observers SS and YS) show the results with 20% contrast modulations.

they were substantially reduced (or absent) when the modulation amplitude was 20% (the inset graphs in Fig. 5, shown for observers SS and YS). Thus, the analyses of P_1, P_1 gain, and the CV resonance dip consistently indicate that 30% and 40% contrast modulations were effective, whereas 20% modulations were too weak for inducing stochastic resonance in the mechanisms that control perceptual alternations in binocular rivalry.

Because the matching of the resonance frequency to the average spontaneous alternation rate is a critical signature of stochastic resonance, we verified this property in greater detail. It is known that image alternation rates gradually slow during the course of a

continuous observation of binocular rivalry, presumably due to concurrent contrast adaptation (e.g., Lehky, 1995; Suzuki & Grabowecky, 2004). We thus split each trial into the first and second halves and examined those separately. As expected, the alternation rates slowed in the second half-trials; we note that, though the alternation rates gradually slowed within each continuous-viewing trial, the average rates did not slow across trials; apparently, the 2 min break inserted between trials was sufficient to induce recovery from contrast adaptation (see also Suzuki & Grabowecky, 2004).

The critical prediction was that the resonance frequency (i.e., the contrast-modulation frequency that
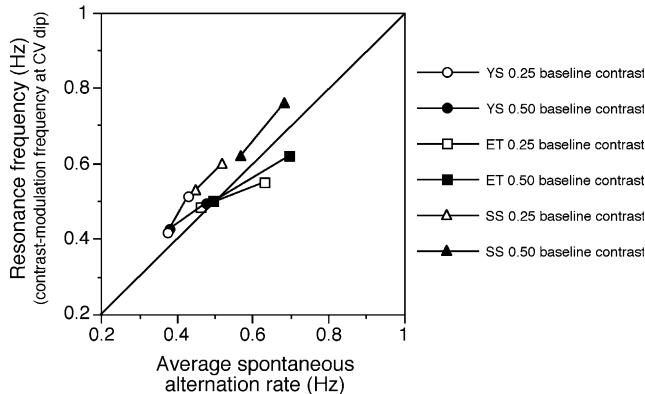
Fig. 6. The relationship between the resonance frequency (the contrast-modulation frequency that minimizes CV) and the mean spontaneous alternation rate. A positive correlation is apparent ($r^2 = 0.735$). Furthermore, the data points lie close to the diagonal (with slope = 1), indicating that the resonance frequency closely followed the average spontaneous alternation rate while the latter varied due to individual differences, the use of different baseline contrasts (0.25 or 0.50), and the within-trial slowing of binocular rivalry. Connected pairs of symbols represent the first half-trials (upper right) and the second half-trials (lower left) for each baseline contrast for each observer.

minimized the CV) should follow this within-trial slowing of the spontaneous alternation rate. Fig. 6 plots the relationship between the resonance frequency and the average spontaneous alternation rate. Each pair of connected symbols represents the first half-trials (upper right symbol) and the second half-trials (lower left symbol) for each observer under each baseline contrast shown in Fig. 5. Note that all pairs have positive slopes that lie in the vicinity of the diagonal with a slope of 1, indicating that the resonance frequency followed the within-trial slowing as well as other variations in spontaneous alternation rates due to different baseline contrasts and individual differences.

4. Discussion

To understand how neural adaptation and inhibitory interactions are coupled with noise to generate spontaneous perceptual alternations in binocular rivalry, we investigated whether the underlying system supported a specific noise-mediated phenomenon known as stochastic resonance. We confirmed this by demonstrating: (1) that the maximum resonance occurred in perceptual switching when the frequency of the applied periodic signal matched the average rate of spontaneous perceptual switching, and (2) that the distribution of perceptual-dominance durations exhibited multiple resonance peaks at the odd-integer multiples of the half-period of the periodic signal.

4.1. Constraining computational models

Existing computational models have been successful in explaining the detailed time-averaged behavior of binocular rivalry (see Laing & Chow, 2002, for a review). In contrast, those models have not been tested rigorously with respect to their dynamic behavior, primarily due to a lack of stringent behavioral constraints on the dynamics of binocular rivalry. The apparently stochastic time series and the Gamma and/or log-normal shape of dominance-duration distributions did not pose rigorous challenges because most models could fit these properties by adding random noise and adjusting the parameters of adaptation and/or inhibitory interactions. Our demonstration of stochastic resonance in binocular rivalry (in particular the characteristic peaks in the dominance-duration distributions at the odd-integer multiples of the contrast-modulation half-period) provides strict dynamic constraints as well as insights into the roles of adaptive and inhibitory neural interactions, internal noise, and a threshold, in generating spontaneous perceptual switching.

To illustrate these points, we examined behaviors of representative models of binocular rivalry that have been developed to simulate the dynamics of perceptual switching. In particular, we contrasted the astable multivibrator model (Lehky, 1988), based on a Schmitt trigger that exhibits stochastic resonance (e.g., Gammaitoni et al., 1998; Melnikov, 1993), with often-cited winner-take-all models of the type developed by Wilson (Wilson, 1999, 2003; Wilson, Krupa, & Wilkinson, 2000; Wilson, Blake, & Lee, 2001) and Mueller (1990). These models basically capture macroscopic aspects of the spiking neuronal network developed by Laing and Chow (2002). Whereas simulating large populations of neurons (as in a spiking neuronal network model) is beyond the scope of this primarily empirical study, simplified models are suited for deriving analytical inferences. The comparative analyses of the three representative models provide insights into how our empirical results constrain models of the mechanisms underlying perceptual switches in binocular rivalry.

Despite their critical differences, it is assumed in all three models that spontaneous perceptual switching is primarily driven by neural adaptation and inhibitory interactions described by the following differential equation:

$$\tau \frac{dE_A}{dt} = [sign_A] \bullet E_A + f_A(S_A, H_A, I_B), \qquad (1)$$

where the two rivaling images are labeled by A and B, E_A is the activation (or excitation) of the A-unit (preferentially responsive to image A), S_A is the strength (e.g., contrast) of image A, H_A is the slow self-adaptation (or habituation) of the A-unit, I_B is the inhibitory input from the competing B-unit, and τ is the time constant of primary adaptation. The dynamics of the B-unit (E_B) are given by exchanging the A and B labels.

The three models differ in terms of (1) whether or not adaptation ([sign] = −1) and recovery-from-adaptation ([sign] = +1) are yoked to perceptual dominance, (2) the exact forms of contrast response, adaptation, and inhibitory interactions—embedded in the $f_A(S_A, H_A, I_B)$ term, and implementations of perceptual non-linearity (i.e., how the all-or-none perceptual transitions between the competing images are implemented). We compared these representative models (Lehky, 1988; Wilson, 2003, and its predecessors; and Mueller, 1990) in terms of whether or not they could generate stochastic resonance, and how that depended on their specific implementations of adaptation, inhibitory interactions, noise, and/or perceptual non-linearity.

4.2. The astable multivibrator model (Lehky, 1988)

In this model, it is assumed that the state of perceptual dominance determines whether competing neurons adapt or recover from adaptation. For example, when image A is perceptually dominant, the A-unit adapts (i.e., $[sign_A] = −1$) while the B-unit recovers from adaptation (i.e., $[sign_B] = +1$). Influences of self-adaptation, stimulus strength, and inhibitory interactions are all subsumed in the term, $[sign] \bullet E$; thus, the parameters H (slow self-adaptation), S (direct stimulus input), and I (competitive inhibition) are not explicit in this model. To implement the contrast modulations of the competing images, we made a simple assumption that increasing the strength of one image has a proportional inhibitory influence on the units responding to the competing image. That is

$$f_A(S_A, H_A, I_B) = -I_B = -I \bullet \Delta S_B, \qquad (2)$$

where ΔS_B is a change in the strength of image B (relative to some default value), and I is a constant that scales stimulus strength to an inhibitory neural influence. The A and B labels can be exchanged to obtain the equation for f_B.

Except for the added inhibition term, $-I \bullet \Delta S_B$ (inhibition of the A-unit from the B-unit) and $-I \bullet \Delta S_A$ (inhibition of the B-unit from the A-unit), the formulation is identical to the original astable multivibrator model (Lehky, 1988). Note that increasing (or decreasing) the contrast of image B decreases (or increases) the activity of the A-unit (E_A) due to the $-I \bullet \Delta S_B$ term, while increasing (or decreasing) the contrast of image A decreases (or increases) the activity of the B-unit (E_B) due to the $-I \bullet \Delta S_A$ term. Thus, this modified astable multivibrator model obeys Levelt's 2nd proposition (increasing [or decreasing] contrast of one image decreases [or increases] the dominance duration of the other image). As in Lehky (1988), a random-walk noise, $D \bullet \delta$ (D is noise intensity and δ randomly assumes −1 or +1 at each time update $t + \Delta t$ [where

$\Delta t \ll \tau$] in our Euler numerical simulation),[4] is directly added to the differential equations for the neural responses (E_A and E_B) representing the competing stimuli.

The all-or-none characteristic of perceptual switching between the competing images A and B is implemented by a threshold. For example, when image A is perceptually dominant, the A-unit adapts and the B-unit recovers from adaptation. Image A remains dominant until the activity of the A-unit falls to threshold. At that point, image B becomes perceptually dominant.

In simulating our results, we first fit the control condition (e.g., the leftmost distribution in Fig. 3) using τ and D as the fitting parameters.[5] We then implemented the square-wave contrast modulation as, $\Delta S(t) = h \bullet SW(f, \phi, t)$, where h corresponds to the neurally transduced amplitude[6] of the contrast modulation, and $SW(f, \phi, t)$ flips between −1 and +1 with a specific frequency f and phase ϕ (180° apart for the two images). As shown in Fig. 7, the astable multivibrator model produces a good fit for both the odd-integer multiple peaks and the relative height of those peaks, with h used as the only fitting parameter.

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[4] We used random-walk noise because it was the form of noise used in Lehky (1988). Random-walk noise is a discrete version (i.e., randomly assuming two discrete values without intermediate values) of random noise. The two forms of noise are virtually equivalent for our purposes because the time steps we used for updating noise were orders of magnitude smaller than τ and the contrast-modulation frequency (i.e., both forms of noise effectively approached normal distribution in the time scale of perceptual alternations). Furthermore, induction of stochastic resonance should not depend on the form of noise being random-walk or random. We also verified that the use of random noise did not change our results.

[5] To produce good fits to the control distributions with the astable multivibrator model, we let τ diminish monotonically starting at the beginning of each dominant percept (this is equivalent to assuming initially accelerated adaptation relative to exponential). This manipulation, however, was not crucial for this model to produce the multiple stochastic-resonance peaks. τ was a constant parameter for fitting with Mueller (1990) and Wilson (2003), but these models had more free parameters than the astable multivibrator model to fit the control distributions. We imposed a refractory period (the minimum time required to complete a perceptual switch) to avoid unrealistically rapid perceptual switches and to improve fits for all three models. In the astable multivibrator and Mueller (1990) models, the unit of time is arbitrary. Thus, when we fit these models to the control distributions, we scaled the mean of the simulated data to the mean of the actual data. For all models, we ran 1500–5000 simulated perceptual switches to fit each dominance-duration distribution.

[6] Because the visual system responds strongly to transient changes in luminance, it is possible that the primary influences of contrast modulation occur at the rising and falling edges of the square-wave modulation. Thus, in fine-tuning the fits, we set h to zero except for a specified duration following the rising and falling transitions of the square-wave; this duration was adjusted to improve the overall fit, but it was kept constant across all contrast modulation frequencies. The implementation of transient responses improved fits in some cases, but it was not critical for producing the odd-integer multiple peaks.
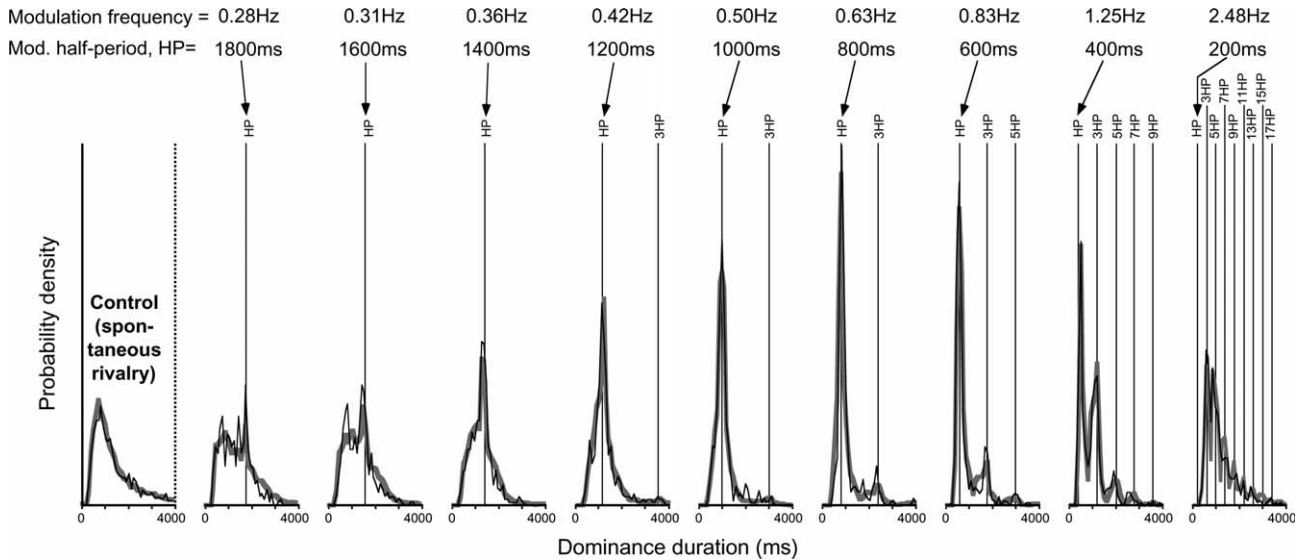
Fig. 7. Fitting the dominance-duration distributions for contrast-modulation frequencies from 0.28 to 2.48 Hz (with the corresponding half-periods [*HP*] from 1800 to 200 ms), using the astable multivibrator model based on a Schmitt trigger (known to exhibit stochastic resonance). The thin curves show the data and the thick curves show the fits. Note that the locations of the peaks at the odd-integer multiples of the modulation half-period (indicated by the vertical lines), the number of the peaks, and the relative amplitude of the peaks are simulated reasonably well. Observer YS's data for 0.50 baseline contrast (blinking allowed) are shown as an example. The fits to other data are similar.

4.3. Winner-take-all model 1 (Wilson, 2003,[7] and its predecessors)

In these models, the [*sign*] factor in Eq. (1) is always −1; the primary adaptation factor is thus not yoked to perceptual dominance. Because these models were partly designed to reflect the neurophysiology of the visual system, they use an elaborated form of $f_A(S_A, H_A, I_B)$, including implementations of H_A (self-adaptation), S_A (direct stimulus input), and I_B (competitive inhibition). We have:

$$f_A(S_A, H_A, I_B) = \frac{100 \bullet (\max[\{S_A - g \bullet I_B\}, 0])^2}{(10 + H_A)^2 + (\max[\{S_A - g \bullet I_B\}, 0])^2},$$
(3)

$$\tau_I \frac{dI_B}{dt} = -I_B + E_B,$$
(4)

$$\tau_H \frac{dH_A}{dt} = -H_A + b \bullet E_A,$$
(5)

where τ_I and τ_H are the time constants of inhibitory interactions and slow self-adaptation, respectively, and max[*X*, *Y*] returns the larger of the two values, *X* and *Y*. The A and B labels can be exchanged to obtain the equation for f_B. Levelt's 2nd proposition is obeyed because of the competitive inhibition term, I_B.

The all-or-none characteristic of perceptual switching is implemented by a winner-take-all rule. Perceptual dom-

inance is determined by the relative strength of the A-unit and B-unit; that is, image A is perceptually dominant when $E_A > E_B$ and image B is perceptually dominant when $E_B > E_A$.

As with the astable multivibrator model, we added noise directly to the differential equations for E_A and E_B. Because perceptual dominance is determined by the relative activity of E_A and E_B (the neural units responding to the competing stimuli), fluctuations in their activity seem to be the natural locus of the relevant noise influencing perceptual switches.

We first fit the baseline conditions using S_A, S_B, τ, τ_I, τ_H, b, g, and D as the free parameters. We then implemented the square-wave contrast modulation as $S(t) = S + h \bullet SW(f, \phi, t)$, where S is the baseline contrast and h is the contrast-modulation amplitude. As with the astable multivibrator model, we used h as the free parameter to fit the odd-integer multiple peaks. We were unable to obtain the primary or higher-order stochastic resonance peaks. Nor were we able to obtain the asymptotic behavior, that is, we were unable to obtain the strong peak expected at the contrast-modulation half-period when the amplitude of the modulation was 100% (i.e., presenting the left-eye and right-eye images sequentially).

Note that, in Wilson's model, the locus of noise could be other than the responses of the competing neural units. We verified that this model could simulate Gamma-like spontaneous dominance-duration distributions whether the noise was added to the responses of the competing neural units (i.e., to the differential equations for E_A and E_B—Eq. (1)), to adaptation of these units (i.e., to the differential equations for H_A

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[7] We used only the 1st stage of the model; the 2nd stage would have been redundant because the pattern presented to each eye was constant in our study.

and H_B—Eq. (5)), or to their inhibitory interactions (i.e., to the differential equations for I_A and I_B—Eq. (4)). Wilson's model simulated our data well when the noise was added to the *adaptation* equations. Adding noise to the inhibitory-interaction equations also produced some of the resonance peaks and the asymptotic behavior, but the quality of fit was inferior (e.g., we failed to produce more than two resonance peaks). Furthermore, although adding noise to the adaptation equations for H (affecting the speed of adaptation) produced good fits to our data, adding noise directly to the H term in Eq. (3) (affecting the impact of adaptation) failed to produce the resonance peaks or the asymptotic behavior. Thus, if Wilson's model captured the underlying mechanisms of perceptual switching, the noise must primarily affect the speed of adaptation of the competing neural units.

4.4. Winner-take-all model 2 (Mueller, 1990)

This model is overall similar to Wilson (2003) with differences in the forms of the contrast-response function (logarithmic rather than Naka–Rushton) and inhibitory interactions:

$$f_A(S_A, H_A, I_B) = \ln(S_A) - a_A\left(1 - c_A\frac{\ln(S_A)}{\ln(100)}\right) \bullet I_B - H_A,$$
(9)

$$I_B = \max[E_B, 0],$$
(10)

$$\tau_H \frac{dH_A}{dt} = H_A + b \bullet \max[E_A, 0],$$
(11)

where $\max[X, Y]$ returns the larger of the two values, X and Y. The A and B labels can be exchanged to obtain the equation for f_B. Levelt's 2nd proposition is obeyed because of the competitive inhibition term, I_B, which is directly proportional to activation of the competing B-unit.

As with Wilson (2003), the all-or-none characteristic of perceptual switching between the competing images A and B is implemented by a winner-take-all rule (i.e., image A is perceptually dominant when $E_A > E_B$ and image B is perceptually dominant when $E_B > E_A$).

We first fit the baseline conditions using S_A, S_B, τ, τ_H, a_A, a_B, b, c_A, c_B, and D as free parameters (note that $S_A = S_B$, $a_A = a_B$, and $c_A = c_B$ as in Mueller, 1990), and then implemented the square-wave contrast modulation as $S(t) = S + h \bullet SW(f, \phi, t)$. The simulation results were similar to those for Wilson (2003). When the noise was added to the differential equations for the neural responses, we were unable to obtain the resonance peaks or the asymptotic behavior. When the noise was added to the differential equations for adaptation Eq. (11), we were then able to fit the data well.

In summary, while all three dynamic models of perceptual switching are consistent with Levelt's 2nd proposi-

tion and the general double-well-potential framework, and they can simulate Gamma-shaped dominance duration distributions from spontaneous binocular rivalry, our stochastic resonance results provide additional insights into their implementations of noise and all-or-none perceptual switching. The success of the astable multivibrator model (Lehky, 1988) suggests that the mechanisms underlying perceptual switches might be characterized by simple linear interactions among stimulus input, adaptation, inhibitory modulations, and response noise of the competing neural units, with threshold crossing being the source of all-or-none perceptual switching.[8] Alternatively, our simulation results with Wilson's (2003) and Mueller's (1990) models suggest that if the mechanisms of perceptual switches are characterized by a winner-take-all algorithm coupled with the non-linear interactions among stimulus input, adaptation, and inhibitory modulations implemented in these models, the locus of the critical noise must be in the speed of adaptation rather than in the responses of the competing neural units. Future neurophysiological research might resolve these alternatives by investigating (1) whether perceptual switches are initiated by the reduction to threshold of the activity of the neural units responding to the currently perceptually dominant image or by changes in the sign of the relative activity of the competing units, and (2) whether the rate of perceptual switches is primarily influenced by the response noise in the competing neural units or by fluctuations in the speeds of their adaptation.

4.5. Estimating the internal noise influencing perceptual switching

Our results also provide insights into the nature of the internal noise that contributes to perceptual switching. In particular, the magnitude of resonance (i.e., the size of the CV dips shown in Fig. 5) depended on the relative rather than the absolute amplitude of contrast modulation. In all of the experiments reported here, the contrast was modulated between the baseline contrast and a reduced contrast. If we define the percent contrast modulation as,

Percent contrast modulation

$$= \frac{[\text{baseline contrast}] - [\text{lower contrast}]}{[\text{baseline contrast}]} \times 100\%,$$

contrast modulations of 30–40% clearly produced resonance (see the primary graphs in Figs. 4 and 5), whereas the P_1, P_1 gain, and resonance dips were all weak or absent with 20% modulation (see the inset graphs in Figs. 4 and 5).

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[8] We verified the importance of threshold crossing in the astable multivibrator model by demonstrating that the model failed to produce the resonance peaks (except for the primary peak) when the algorithm for perceptual switching was changed from threshold-crossing to winner-take-all.

Two points are noteworthy. First, both 30% and 20% contrast modulations were clearly visible, suggesting that both levels of contrast modulation were above threshold, that is, they were greater than the sensory noise that limits detectability of contrast modulation. This in turn suggests that the system that controls perceptual switching in binocular rivalry has its own noise and threshold which are greater than the sensory noise and threshold that control the visibility of contrast modulations. The fact that 30% contrast modulation clearly produced stochastic resonance but 20% modulation did not, also provides a signal-based estimate of the magnitude of the relevant internal noise, equivalent to somewhere between 20% and 30% of contrast modulation.

Second, the strength of resonance (i.e., the size of resonance dip) was similar for rather different *baseline* contrasts, 0.50 and 0.25, as long as the *percent contrast modulation* was the same (Fig. 5). We subsequently verified this ratio-wise (divisive) normalization of the perceptual-switching mechanisms to these baseline contrasts for a wide range of contrast-modulation amplitudes (0–100%). Thus, internal noise, threshold, and gain of the contrast modulation appear to be calibrated to the baseline contrast in such a way that the mechanisms underlying perceptual switches respond to the proportion of contrast modulation (at least when different baseline contrasts are blocked, allowing time for the visual system to adapt to the baseline contrast).

5. Summary

We have demonstrated internal-noise based stochastic resonance in binocular rivalry by applying weak periodic contrast modulations to the competing images. Spontaneous perceptual switches in binocular rivalry have been thought to be mediated by interactions among stimulus input, neural adaptation, mutual inhibition, and noise that together generate competing marginally stable states consistent with a double-well potential framework. Our results have shown that these interactions must occur in such a way that the system supports stochastic resonance. Our computational simulations have shown how this stochastic-resonance requirement constrains the current dynamic models of binocular rivalry in terms of the locus of the relevant noise and the algorithm of perceptual switching. The results also suggest that the magnitude of the internal noise involved in perceptual switches is equivalent to approximately 20–30% of contrast modulation, and that the locus of this noise is beyond the processing stage where sensory noise influences pattern detection. Because the noise magnitude appears to calibrate to baseline contrast, it is possible that the magnitude of internal noise might be adaptively maintained in the brain such that it is low enough to prevent hyper-sensi-

tive responses to small fluctuations in the environment (thus providing sufficient time and stability to analyze each perceptual interpretation), but high enough to keep the system from getting mired in a single state.

Acknowledgments

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