

# Percept-switch nucleation in binocular rivalry reveals local adaptation characteristics of early visual processing

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When the two eyes view incompatible images that subtend the entire visual field, perception alternates between the two images unpredictably: at seemingly random times and locations, observers experience sudden changes in the awareness of the unchanging visual stimulation. Here we focus on the very first spontaneous breakout from the very first suppression phase after onset of the two eyes' competing whole-field stimuli. We call such spontaneous local breakout an "initial percept-switch nucleation." We employed *homogeneous* visual input to examine where, and how, spontaneous local *initial percept-switch nucleations* originate, demonstrating that their spatial distribution contains locally random inhomogeneities, which are eye- and observer-dependent. We were able to predict the occurrence probability of the percept nucleations by adaptation buildup of the neurons associated with the representation of one eye's image. Intriguingly, the neuronal processes related to both cross-inhibition and local eye dominance could not predict nucleation probability; this is because nucleation inhomogeneity appeared to be different from another previously reported local inhomogeneity known as "onset bias" signifying the local first *dominance-choice inhomogeneity* upon stimulus onset. Collectively, we reveal a governing role of local adaptation in the neurons associated with early visual processing of one eye's image, in the origination of new phases in awareness.

Keywords: visual awareness, bistable perception, ambiguous perception, percept-switch nucleation

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## Introduction

Visual perception automatically alternates between alternative interpretations when there is inconclusive sensory input. When the two eyes view incompatible stimuli, perception alternates between the two eye's images: this is called "binocular rivalry." This phenomenon is important: it provides a window on the formation of visual awareness because perception alternates while the visual input is constant. Interestingly, when the two eyes' images subtend an extended fraction of the visual field, the perceptual alternations occur randomly throughout the visual field: Despite unchanging visual stimulation, observers often experience that a percept alternation starts as a sudden *local* percept switch, which then spreads outward. Such a process poses the fundamental question: which signal in the alternation process is responsible for the randomly emerging percept switches?

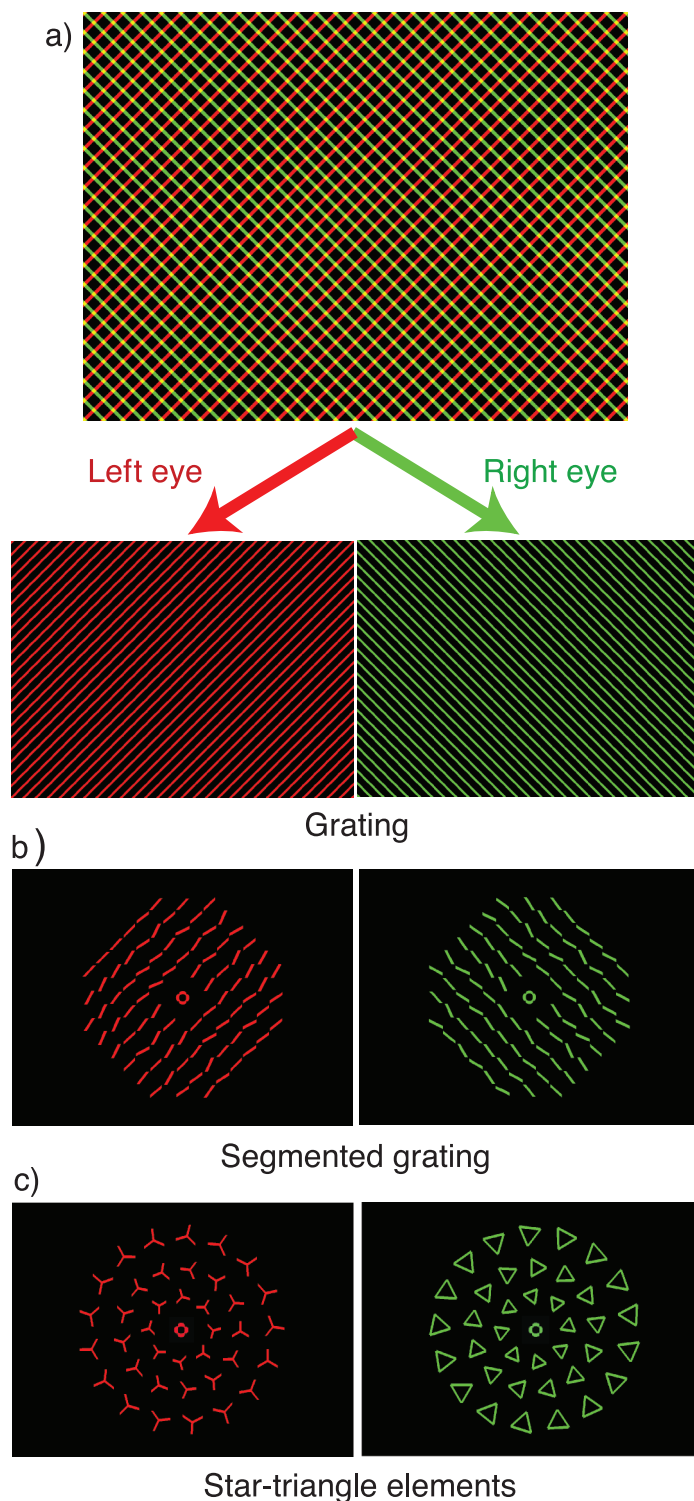
Suddenly emerging local perceptual changes can be observed in [Figure 1](#), where percept switching originates as a local change in the perceived line orientation. Percept

switches in binocular rivalry can be regarded as a transition in the neuronal state that encodes the local current percept. Here we call the sudden local breakout from suppression that initiates a percept switch as a "percept-switch nucleation" (by analogy with nucleations in physics, where nucleation denotes a sudden local change in the physical state of a material, e.g., in raindrop formation or sudden atomic spin reorientation in magnetism). Visual percept switches are governed by neural processes involving network activity occurring on time-scales up to several seconds. This lucky situation enables us to directly *perceive* the nucleations for ourselves and score the location and time at which they occur.

Where a percept-switch nucleation originates, and how the newly formed local percept propagates, is now beginning to be uncovered for the (non-generic) case when the percept changes are triggered by the experimenter using spatially inhomogeneous visual input (Kang, Heeger, & Blake, 2009; Knapen, van Ee, & Blake, 2007; Lee, Blake, & Heeger, 2005, 2007; Naber, Carter, & Verstraten, 2009; Paffen, Naber, & Verstraten, 2008; Wilson, Blake, & Lee, 2001). The fundamental question of where, and how, in a

homogeneous unbiased 2D visual field a percept-switch nucleation arises spontaneously has not yet been addressed systematically. This is an important fundamental question because it forms a novel window on the underlying neural processes associated with percept formation.

We are particularly interested in the very first spontaneous breakout from the very first suppression phase after



onset of the two eyes' competing whole-field stimuli. We call such spontaneous local breakout as an “initial percept-switch nucleation,” forming a well-controlled window because the conditions for those *initial percept-switch nucleations* can be determined by the experimenter.

Note, thus, that the *initial percept-switch nucleations* should not be confused with the very first choice preference in image dominance upon the sudden synchronous onset of the two eyes' competing images, known as “onset bias” (Carter & Cavanagh, 2007). This choice process is also known to be inhomogeneous as there are considerable *onset biases* for one or the other eye's stimulus in different local portions across the entire visual field (Carter & Cavanagh, 2007). An *initial percept-switch nucleation*, on the other hand, happens at the start of a developing rivalry situation, being a switch process that is not necessarily associated with the choice process involved in onset bias (in this paper, we will indeed see that it is not related).

We explore the location and time of *initial percept-switch nucleations* for homogeneous, unbiased visual fields. The whole-field pattern of gratings in Figure 1a, used for introductory illustration, turned out to be suboptimal for experimentation. Although successive percept alternations occur roughly every 1.5 s, they often appear to start simultaneously along a large part of a line, making it difficult to indicate where they originate. This is

Figure 1. (a) When the two eyes view an extended field of orthogonal gratings, the process of binocular rivalry produces continuously emerging percept-switch nucleations of locally dominant red or green domains of differently oriented lines. The number of nucleations increases with larger images, i.e., by viewing these images from a relatively short distance. A nucleation in binocular rivalry can be regarded as a local phase transition in the state of the neurons associated with the current awareness phase. After closing one eye for 3 s (say, the left eye stimulated with the red pattern, and keeping the open eye fixed in the center of the green pattern), flash suppression can be experienced upon opening the left eye: the monocularly viewed (green) pattern is then completely suppressed by the newly visible (red) pattern. After several seconds, random nucleations of the green grating break out from suppression through the red pattern. This can be experienced using red–green goggles in the superimposed gratings in the top panel. For the other stereo pairs, free fusion suffices. A whole-field pattern of gratings can produce quite a few local phase transitions making it challenging to keep track of the number of nucleations. (b) This grating stimulus subtends a smaller retinal area and it contains segments with spatially jittered orientations that slow down nucleation-induced phase changes. (c) A pattern of distinct symbols slows down nucleation-induced phase changes to the extent that all observers are able to keep track of the emerging nucleations. A benefit of this stimulus is that elements become larger with eccentricity, thereby taking into account peripheral decreased visibility.

due to the fact that the new percept propagates relatively fast along a continuous straight line, compared to hopping from one line to the next. This is in accordance with the physiology of interactions between neurons that are organized in orientation columns (Ohki, Chung, Ch'ng, Kara, & Reid, 2005); indeed, the perceptual effect has been quantified psychophysically (Arnold, James, & Roseboom, 2009; Maruya & Blake, 2009; Nichols &

Wilson, 2009). The stimulus in Figure 1b, consisting of a segmented grating with spatially jittered line orientations, substantially reduces these problems of perceiving where a percept-switch nucleation occurs. In the experiments reported below, we started out using an even more controlled local symbol stimulus: a whole-field star-triangle stimulus (Figure 1c). We used an established technique called “Flash Suppression” (Wolfe, 1984; see

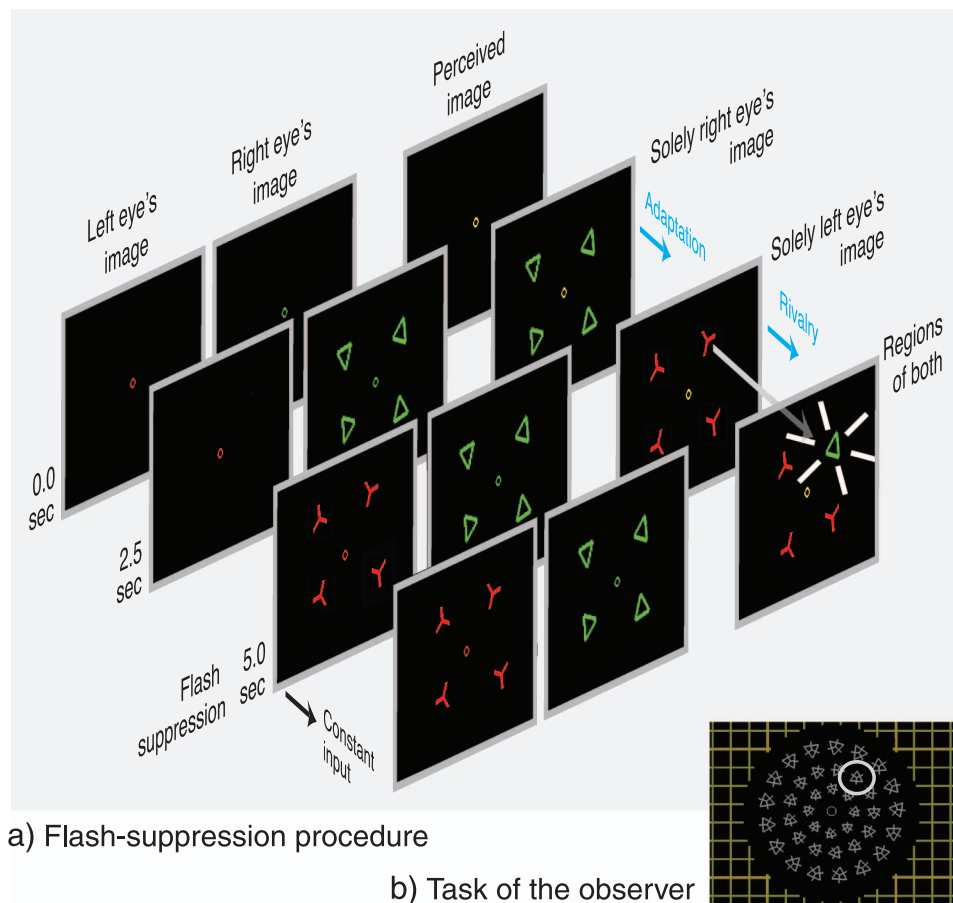


Figure 2. (a) Time series of stimulus presentation, employed to produce, first, flash suppression and then a perceived local nucleation (denoted by white highlighting stripes) where the suppressed monocular stimulus (here the triangle in the green right eye's image) breaks out of suppression and replaces the dominant (red star) stimulus. For clarity, only a few stimulus elements are depicted. At the beginning of each trial, only a binocular fixation circle and a binocular grid were shown. A subject was instructed to fixate the circle throughout a trial. After 2.5 s, one eye's stimulus was presented, while only the fixation circle and the stabilizing grid (for clarity, not depicted) were shown to the contralateral eye. This image was presented for 2.5 s to achieve adaptation. Then, the other eye's image was additionally presented for 5 s. Upon presentation of this other eye's image, awareness of the whole visual field reverses in a single flash to this (non-adapted) image. This is also the moment that binocular rivalry sets in because the two competing images are both present. Here, in this figure, it is the complete green image that becomes adapted. Then, subsequently the red image flash suppresses the green image completely. In the competition for visual awareness, there will be one first location where a nucleation breaks out from a “red Y-shape dominance phase” to a “green triangle dominance phase.” Subjects reported the instant of the first nucleation by hitting a key. (b) After 5 s into the nucleation-evoking binocular rivalry period (meaning 10 s from the beginning of the trial), the stimulus became gray and subjects then reported the location of the first nucleation by placing a circle at its (remembered) location. To reduce aftereffects during this part of the task, the stimulus became low contrast gray and both eyes were presented with the same stimulus. To further reduce aftereffects upon the next trial, the stimulus was rotated by 7.5 deg.

also Figure 2) to ensure that the percept preceding the measured nucleation events is the same at all local elements and starts at the same time.

## Materials and methods

### Apparatus

#### Anaglyphic setup

The stimuli were back-projected by a projector on a large screen ( $2.2 \times 1.6$  m;  $58 \times 45$  deg;  $1024 \times 768$  pixels; at 75 Hz) at 2-m viewing distance. To enable the presentation of large images to the two eyes, we utilized a conventional red–green anaglyphic technique. Note that by using this technique the two half-images were superimposed and projected onto corresponding retinal locations under natural vergence eye posture for the viewing distance used. The intensities of the red and green half-images were adjusted (via the numbers for the color lookup table for the video card) until they appeared equiluminant when viewed through the red and green filters ( $1.3 \text{ cd/m}^2$ ). The room was completely dark. The incremental luminance (relative to the background and without filters in front of the eyes) of the red stimuli was  $1.5 \text{ cd/m}^2$ , and of the green stimuli it was  $1.9 \text{ cd/m}^2$ . The red and green filters were custom-made (Bernell, Belgium) so that their transmission spectra matched the emission spectra of the red and green stimuli as well as reasonably possible. Photometric measurements showed that minute amounts of the green and red lights leaked through the red (0.4%) and green (0.2%) filters, respectively. A chin rest was used to minimize head movements.

#### Stereoscope

In Experiment 2, where we focused on nucleation time (for which we did not need large visual field presentation), we presented the stimulus dichoptically using a stereoscope. The visual field for each eye was 20 (horizontal) by 30 (vertical) deg (viewing distance 57 cm;  $1600 \times 1200$  pixels; at 85 Hz).

### Visual stimuli

#### Two-dimensional whole-field star–triangle pattern

This stimulus (Figures 1c and 3a) had a diameter of 30.6 deg and consisted of 38 individual star–triangle pairs (each symbol drawn with a line thickness of 6 arcmin). Line elements were locally orthogonal—i.e., unmatchable—in the two eyes' images. The stimulus was presented within an aperture (38.6 deg diameter) of a grid that served to stabilize eye posture (Figure 3a). Locally, every triangle had a deviation in orientation that was randomly drawn from a set  $[-30, +30 \text{ deg}]$ , keeping line segments locally orthogonal in the two eyes. To compensate for reduced

visibility in the periphery, the element magnification factor was 1.4, based upon our own assessment for this specific stimulus, dovetailing nicely with existing accounts that used a factor of 1.3 (e.g., Horton & Hoyt, 1991). In fact, the size of elements in the inner circle (radius of 4.9 deg) was 2.0 deg in diameter. The diameter of the elements in the middle circle (radius of 8.7 deg) was 2.5 deg, and for the outer circle (radius of 13.8 deg), it was 2.9 deg. To reduce an effect of retinal adaptation of the previous trial on the next trial, we rotated the complete stimulus pattern by 7.5 deg upon each trial.

#### Two-dimensional whole-field grating pattern

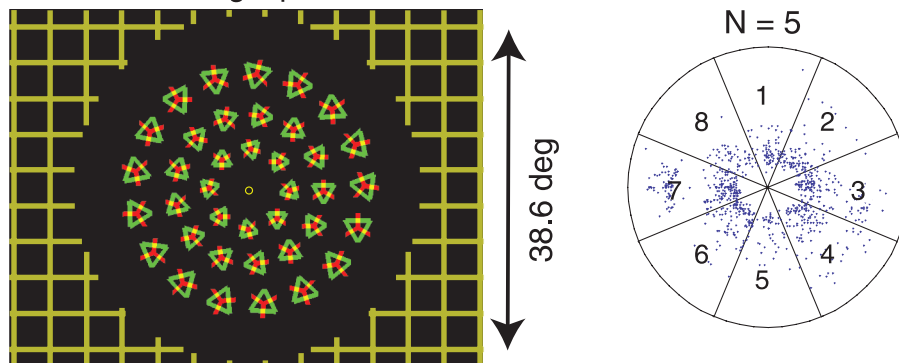
The grating stimulus (Figure 1b; Supplementary Figure 2) had a diameter of 32.6 deg and consisted of segmented lines (segment length of 2.9 deg; gap of 0.4 deg; thickness of 6 arcmin). The gaps served to frustrate the propagation of local dominance of one eye's image over the other, thereby making it easier for subjects to register the origin of separate nucleations. To further slow down this propagation, locally every line segment had a deviation relative to its global orientation (45 deg) that was randomly drawn from a set  $[-30, +30 \text{ deg}]$ . The orientation of the other eye's corresponding line segment was orthogonal, so that locally the two eyes' images were always orthogonal to ensure maximal competition.

#### Four-element star–triangle stimulus

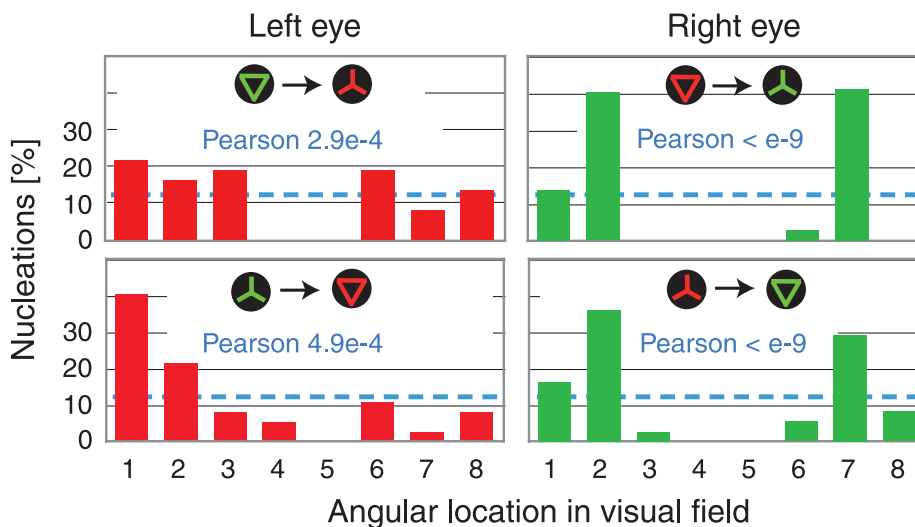
To examine nucleation inhomogeneity across the visual field for a limited set of elements, we presented only four items. There were two types of this stimulus. The stimulus denoted as “central 4-element” had a radius of 4.9 deg with stimulus element size of 2.0 deg (identical to the elements used before), and the “peripheral 4-element” stimulus had a radius of 8.7 deg with element size of

Figure 3. (a) To explore the spatial distribution of nucleations for extended 2D stimuli (whole-field screen  $2.2 \times 1.6$  m;  $58 \times 45$  deg at 2-m viewing distance), we presented anaglyphically (red/green) a pattern of distinct stars in one eye competing with triangles in the other eye. The grid served to stabilize eye posture (aperture diameter of 38.6 deg). The scatterplot contains the scored first nucleations for the five observers. (b) The distributions of nucleations (subject S1) are significantly different from being homogeneous (Pearson  $p < 0.05$ ) for nucleations originating in either eye's representation. Although the distributions have some of their peaks at the same angular segment, they are different, meaning that besides the eye of origin the element shape influences the nucleations. (c) For the 4-element stimulus, an element could occur in 8 pie segments for both the central and peripheral stimuli (icons on the left). The nucleation distributions for both the central and peripheral 4-element stimuli are significantly inhomogeneous (Pearson  $p < 0.05$ ). The distributions for the two eyes are different (Fisher  $p < 0.05$ ) for both the central and peripheral elements, indicating that eye of origin exerts a distinguishing influence.

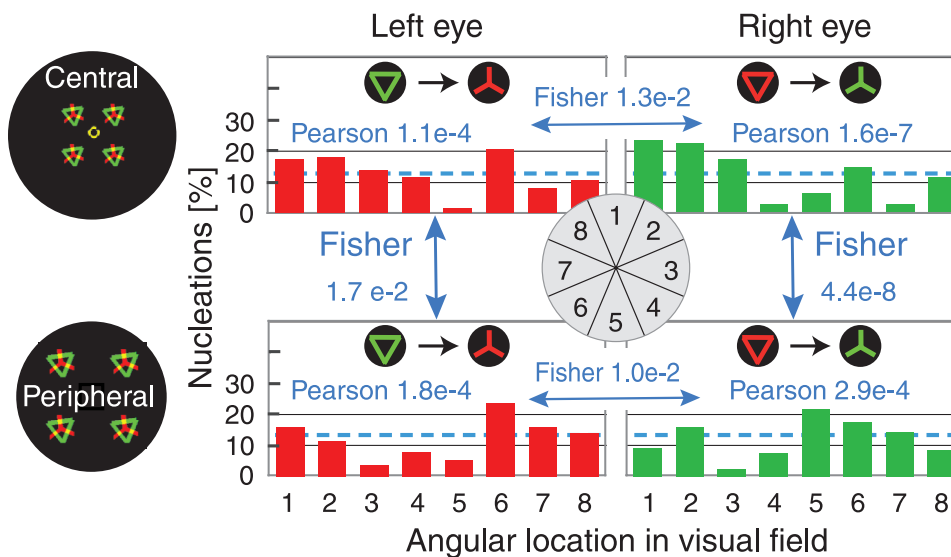
a) Whole-field stimulus and all first nucleations  
Star-triangle pattern



b) Star-triangle pattern (S1)



c) Star-triangle 4-elements (S1)



2.5 deg. Upon each trial, the stimulus was rotated to prevent retinal adaptation. For the same reason, two successive trials started with one color, followed by two trials that started in the other color.

### Surrounding background grid

A whole-field binocularly visible grid (58 by 45 deg; line thickness of 9 arcmin; line distance of 4.5 deg; Figure 3a) and a fixation circle (diameter of 28 arcmin) were continuously present throughout all experiments on the whole-field screen, serving to stabilize fixation of the two eyes. The grid contained an aperture (diameter of 38.6 deg) in which the binocular rivalry stimuli were presented. In the stereoscope, we used the same visual angles for the whole-field grid but this time with a smaller aperture (diameter of 13.4 deg).

### Procedure

To control the beginning of the nucleation process, we used an established technique called “Flash Suppression” (Wolfe, 1984; Figure 2): First, one eye is exposed to an image so that it adapts, then a rivalrous image is added to the second eye, thereby suppressing the first eye’s adapted image. Then, after several seconds, an *initial percept-switch nucleation* breaks out of this suppression. Our subjects pressed a key when the first nucleation appeared, then the stimulus disappeared and the trial ended. After the trial ended, subjects reported the location of this first nucleation by placing a circle at its location. We thus have information both on the timing and on the location of the nucleation. The time sequence of the visual stimulation is given in Figure 2.

A trial block in the experiment using the whole-field stimulus consisted of 24 trials (12 with nucleations starting in the left (red) eye and 12 in the right (green) eye). In addition, we presented four catch trials per trial block in which we imposed a false nucleation at a known location. In such a catch trial, after 500 ms into the binocular presentation period (so after flash suppression had suppressed the initially dominating local stimulus element), the newly presented local stimulus element was faded out to give one location a head start in reappearance. This fading took four refresh frames of the computer monitor meaning that the subjects did not experience this as a transient change in the stimulus. Subjects repeated a trial block six times resulting in 6 times 24 + 4 = 168 trials, each of them causing at least one nucleation and frequently a set of simultaneous occurring nucleations. In the experiment using the 4-element stimulus, there were 132 trials + 10 catch trials. For the separate experiment in which we measured eye movements, we presented 72 trials + 4 catch trials. A trial was always initiated self-paced by the subject. Subjects had the possibility to redo a trial if during the course of a trial an eye blink occurred.

## Results

### Two-dimensional whole-field stimulation

Initial percept-switch nucleations for the 2D whole-field star–triangle stimulus appeared to be scattered inhomogeneously across the visual field (Figure 3a). Because the data differed considerably across subjects ( $n = 5$ ), we first analyzed individual data. We plotted the responses in eight pie segments of the visual field and focused on how these first nucleation scores were distributed across this set of segments. Figure 3b demonstrates that the distributions of nucleation locations of subject S1, separated for element shape and eye, were highly inhomogeneous (Pearson  $p < 10^{-3}$ ; null hypothesis = homogeneity). The results of all subjects revealed strong inhomogeneity (all Pearson  $p < 0.05$  and often  $p < 10^{-9}$ ; 840 nucleations) irrespective of the eye and stimulus shape (statistics of each individual subject in Supplementary Figure 1). Although some roughly similar peaks occur at the same angular segments for the two shapes (e.g., bars 2 and 7 in the green plots of Figure 3b), the distributions are generally different between the stars and triangles (Supplementary Figure 1), meaning that, besides the eye, the element shape also affects nucleation. This latter finding should not be taken to indicate that perceived shape is involved. The event of scoring the location of a percept-switch nucleation goes too fast to be able to perceive the exact shape of the emerging symbol. The reason that the presented line configuration (shape of the element) influences the outcome is that the orientation columns of the local line elements are connected (see discussion above). All subjects were able to detect randomly occurring “catch nucleations,” where we imposed a false nucleation at a known location (the worst subject scored 21 out of 24 correct detections). From the catch trials, we determined the reaction time, which was roughly 450 ms, being sufficiently smaller than the first nucleation time (see Supplementary Figure 1c for individual data).

To test whether our results generalize to other 2D patterns, we examined nucleations for a whole-field orthogonal grating stimulus and again found strong nucleation inhomogeneity and similar temporal properties (Supplementary Figure 2, including Pearson statistics). The similarity of nucleation distributions for both the star–triangle and the grating stimuli within one observer across the months that we ran the experiments was probabilistically larger (probability  $> 0.5$ , Fisher’s exact test, quantifying whether two distributions were drawn from the same set) than the variation in distributions across observers in one experiment session (probability  $< 0.05$ ).

Whenever three or more percept-switch nucleations appeared at the same time, subjects pressed a simultaneity button at the end of the trial. The percentage of trials where an observer indicated “simultaneity” varied between 14% and 37% across observers (Supplementary

Figure 1c for specification per subject). These considerable numbers potentially reflect that the task to register individual nucleations was demanding in engaging attentional capacity.

## Local stimulation

To eliminate potential limitation of attentional capacity, we presented a stimulus containing only four elements (Figure 3c). We also measured eye movements, and we tested three additional subjects ( $n = 8$ ). To reduce an effect of retinal adaptation of the previous trial on the next, the 4 elements were rotated by 45 degrees at each trial, generating actually eight locations where an element could occur. We presented the elements at two eccentricities denoted by “central” and “peripheral.” To compensate for decreased visibility with eccentricity, a local stimulus-element magnification factor of 1.4 was used (the same as used above for the whole-field star-triangle stimulus).

S1’s distribution of perceived nucleations (Figure 3c) was again clearly inhomogeneous (Pearson  $p < 10^{-3}$ ). The left and right eyes’ graphs in Figure 3c represent drawings from different distributions (Fisher  $p < 0.05$ ). This corroborates the previous experiment in that the nucleations demonstrate a strong sign of monocular neural representation. The average time of the first nucleation for the central (peripheral) 4 elements was 1.5 s (1.6 s) for the left and 1.6 s (1.8 s) for the right eye, resembling S1’s nucleation times for the above 2D whole-field star-triangle stimulus. Collectively, for all subjects, we found results that were similar to those of S1, both for Pearson’s and Fisher’s tests (1056 nucleations; see Table 1; for plots, see Supplementary Figure 3). Again, all subjects were able to detect catch nucleations at imposed locations (the worst subject scored 18 out of 20). Comparing the

nucleation distributions at the two eccentricities revealed that 5 out of 8 subjects produced probabilities larger than 5% that the left eye’s nucleations for the central and peripheral rings were drawn from the same distributions. In all, it is clear that the nucleations were not equally distributed over the 2D field: in 28 out of 32 distributions, the distributions were inhomogeneous (Pearson  $p < 0.05$ ). It is also clear that the spatial distributions of nucleations for the left and right eyes’ graphs differ significantly from one another: in 14 out of 18 cases, the red and green distributions are different (Fisher  $p < 0.05$ ). Thus, at least a major fraction of the inhomogeneity in nucleation probabilities appears to be due to inhomogeneity in monocular neural processing.

Eye movement recordings revealed that four subjects complied well to the instruction to maintain fixation throughout the task producing only minute fractions of eye movements that were larger than the size of a visual symbol (Supplementary Figure 3c; 360 nucleations). One subject made quite a few (about 20% of the trial duration) non-allowed eye movements with a magnitude in the order of a symbol size. Interestingly, the correlations of these eye movements with the nucleation locations were insignificant (Supplementary Figure 3c).

## Neural underpinnings of percept-switch nucleation inhomogeneity

### Nucleation as a race between independent local percept durations

To obtain a first restriction on the spatial scale and complexity level of neural processes responsible for the

Nucleation distributions for the 4-element star-triangle stimulus

Subject	Central			Peripheral			Central-peripheral	
	LE Pearson	RE Pearson	LE-RE Fisher	LE Pearson	RE Pearson	LE-RE Fisher	LE-LE Fisher	RE-RE Fisher
S1	1.1e-4	1.6e-7	0.01	1.8e-4	2.9e-4	0.01	0.02	4.4e-8
S2	1.1e-4	7.7e-7	1.1e-5	7.1e-3	1.9e-3	0.01	0.74	2.0e-5
S3	3.8e-5	<e-9	<e-9	1.8e-3	0.06	0.18	0.42	3.7e-7
S4	7.2e-4	1.0e-4	0.02	0.76	0.43	0.64	0.06	0.10
S5	8.9e-3	0.03	2.7e-3	4.2e-7	1.7e-6	2.5e-6	2.9e-3	4.6e-4
S6	<e-9	<e-9	1.3e-4	<e-9	2.4e-8	<e-9	0.01	6.1e-8
S7	0.47	4.8e-4	0.08	7.1e-6	7.6e-4	5.2e-5	0.06	7.5e-3
S8	2.6e-4	0.01	0.06	<e-9	<e-9	<e-9	0.07	3.6e-6

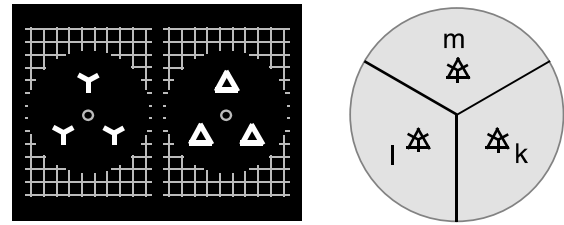
Table 1. The same data as in Figure 3c but for all subjects. The Pearson probability indicates that only 4 (highlighted) out of 32 distributions are homogeneous at a 0.05 probability level. The Fisher coefficients for left eye (LE) and right eye (RE) comparisons (LE-RE) for both the central and the peripheral elements are minute (only 4 exceed 0.05), indicating that the two eyes’ nucleation distributions are different. However, for central and peripheral comparisons within an eye, the Fisher coefficients tend to be slightly larger (two rightmost columns; 6 exceed 0.05), meaning that eccentricity of the elements has a relatively moderate influence.

*initial percept-switch nucleation* inhomogeneity, we first ask: Are there more nucleations in one retinotopic segment simply because there is a purely local bias toward shorter duration of the preceding percept? The underlying process would then be a “race” between *independent* local percept duration processes with time-scales controlled by some to-be-determined neural processing inhomogeneity. In each race, the “winning” location would then be scored as the nucleation site. Alternatively, nucleations could be the result of spatially *interacting* processes of competition and/or cooperation between multiple concurrently active targets.

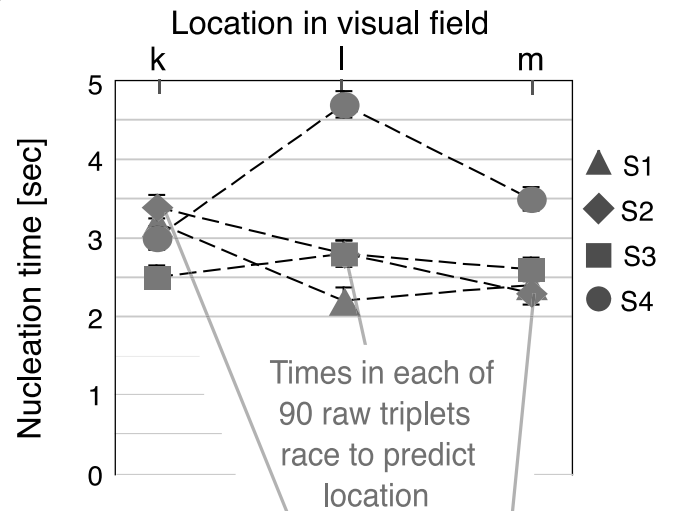
To probe the spatial (in)dependence of percept-switch nucleations, we first measured nucleation times at several locations when each trial contained only *one single* stimulus element: A subset of four subjects scored the nucleation times for three separate angular locations containing competing star–triangle symbols (Figure 4). In this experiment, we presented the stimuli using a conventional mirror stereoscope (see Materials and methods section for details). Triangles were shown to the right eye, which were then flash suppressed by stars in the left eye. We recorded the reappearance time of a triangle in the right eye (in 270 trials). There were 90 presentations for each of the three angular locations (forming 90 triplets). Each location was stimulated in random order to prevent anticipative eye/attention movements. Having thus collected an empirical distribution of single-target nucleations times at each location (their means are plotted in Figure 4b) allowed us to predict (under the hypothesis of *independent* processes) the probabilities that each location would appear as “winner,” and thus become the nucleation location, when measured with 3 concurrently presented targets. We then measured these as usual and correlated the observed with the predicted local nucleation probabilities (both in Figure 4c).

Figure 4. (a) The 3-element stimulus (not to scale) was presented by a stereoscope. Viewing distance was 57 cm; the visual field for each eye was 20 × 30 deg. The aperture diameter was 13.4 deg and the symbols (size of 1.4 deg) were 3 deg from the fixation point. (b) To examine the nucleation time at a single location, we presented a single pair of competing elements. (c) The earliest nucleation time of a triplet from (b) (each triplet consisting of the three possible locations) was used to determine the location of a nucleation. We did so for 90 triplets to predict the spatial distribution of nucleations (gray). In a separate experimental session, the three elements were presented simultaneously and subjects indicated at which location they perceived the first nucleation (black). Comparison of experimental results and predictions reveal a remarkable correlation (note that the *k*, *l*, *m* locations are reordered for clarity). This implies that the local temporal properties of nucleations are for a large part responsible for the spatial distributions of nucleations. (d) The nucleation time increases with monocular stimulus duration employed in the flash suppression paradigm, corroborating the suggestion that adaptation duration is key in the nucleation process.

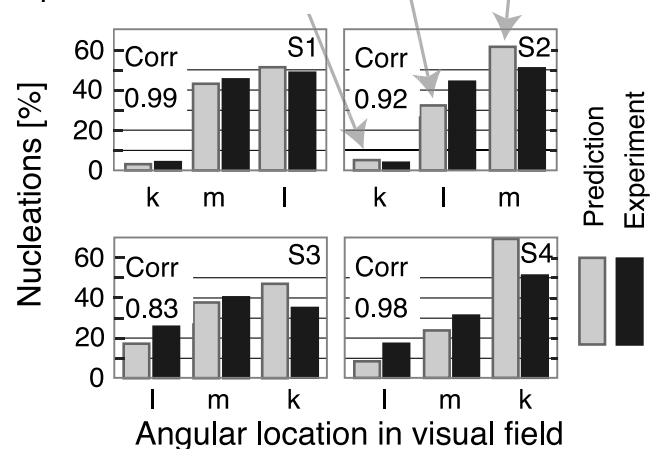
a) Stereoscope stimulus



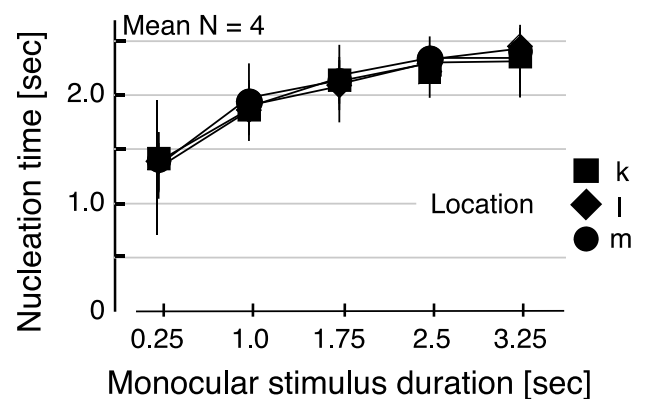
b) Nucleation time



c) Spatial distribution



d) Adaptation build-up





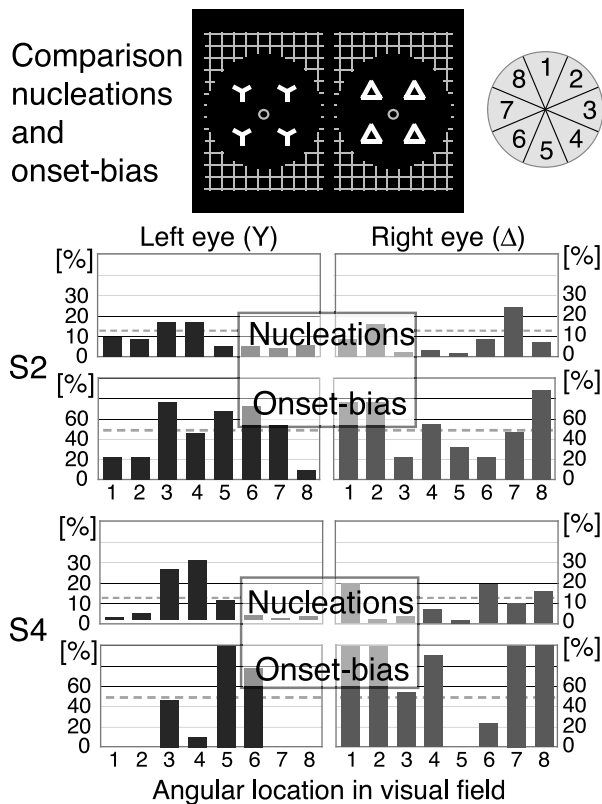


Figure 5. For the relationship between onset bias and nucleation, we presented the 4-element stimulus in the stereoscope (depiction is not to scale). For the onset bias plots, the bars in the left and right panels are complementary, adding up to 100% (no onset bias would mean 50% left and right responses; no nucleation inhomogeneity would mean that all bars are at 12.5%). The results reveal that there is no clear relationship between the inhomogeneous distributions of onset bias and percept-switching nucleations: Spatial segments that contain no onset bias (e.g., segment 7 in S2 or segment 3 in S4) showed, nevertheless, a large difference between the number of nucleations in the two eyes.

The correlation coefficients between the predicted and observed nucleation probabilities are remarkably high ( $>0.83$  for all subjects and  $>0.98$  for two of them; Figure 4c), especially given that our analysis did not include the fact that these correlations will be reduced by the limited accuracy of scoring which of two near-synchronous nucleation events happens first. Indeed, the results for subject S3 show a more moderate correlation, in agreement with a nucleation distribution with much lower inhomogeneity than that of other subjects. Even the unfavorably critical Fisher's test produces for two subjects a probability higher than 0.05 and for S1 even as high as 0.46.

These results clearly support the notion that the inhomogeneous percept-switch nucleation probabilities we measured in all of our main experiments are due to a race between *independent* local percept-switching processes with inhomogeneous local timescales.

## Role of local adaptation buildup

Such local independence may point to early stage adaptation processes as these act locally, and it is widely accepted that they contribute strongly to determining the timescale of rivalrous percept duration distributions (Alais, Cass, O'Shea, & Blake, 2010; Kang & Blake, 2010). To test this role of local adaptation within our nucleation setting, we manipulated the duration of the monocular stimulus parametrically, by repeating the above-mentioned 3-target nucleation experiments using a range of monocular stimulus durations in the flash suppression paradigm (we used monocular exposure durations that were sufficiently long to prevent an effect known as "flash facilitation"; Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007). The nucleation times for all three tested locations increased significantly with the monocular stimulus duration (Figure 4d;  $p < 0.05$ ) and this effect was strong enough to substantially modulate the distribution of nucleation probabilities. These results suggest that local random differences in neural adaptation may govern the observed nucleation inhomogeneities.

Note that the results so far do not exclude a range of other possible neural causes: For example, cross-inhibition (Sengpiel, Baddeley, Freeman, Harrad, & Blakemore, 1998), and many other aspects of inhomogeneous monocular local neural wiring, reflecting local eye dominance, can affect percept durations. Fortunately, we do have the possibility to constrain the potential roles of non-adaptational factors by comparing our nucleation results with another type of rivalry phenomenon that has already been reported to be inhomogeneous: Onset bias in choice preference upon the simultaneous onset of the two eyes' competing images (Carter & Cavanagh, 2007; see also indication of inhomogeneity in an early paper by Crovitz & Lipscomb, 1963, who subjected observers to the onset of two large featureless homogeneous fields with a different color in either eye, reporting inhomogeneous patterns of perceived colors).

## No relation between nucleation and onset bias inhomogeneities

It is, thus, important to include the phenomenon of onset rivalry (Carter & Cavanagh, 2007) in our analyses because adaptation buildup (associated with the presence of the single stimulus in our paradigm) is precisely what distinguishes our initial percept-switch nucleation from onset rivalry. This is because in onset rivalry the two eyes' images are suddenly presented at the same time to a fresh unadapted visual system, whereas in percept nucleation one of the two eyes has already been subjected to an image (and therefore there is adaptation) before the second image is suddenly added. Employing the above specified 4-element stimulus in the same stereoscope as used above (with similar total number trials, i.e., 144 meaning 18 trials

per segment), we examined onset bias for each of the eight angular segments. The experimental procedure is exactly the same as used for the above percept-switch nucleation experiments (in which we presented one eye's image for 2.5 s), except that for the onset bias experiment there is no (0 s) one eye's stimulus presentation. The subject responded in a forced-choice paradigm whether either the left or the right eye's stimulus won in dominance upon the first appearance (no onset bias would mean 50% left and right responses). We did so in 7 subjects, 2 of whom also participated in the experiments above.

Interestingly, while the results replicate the onset rivalry bias inhomogeneity (Carter & Cavanagh, 2007) as well as the above found nucleation inhomogeneity, for none of the subjects there is a relationship between the individual spatial patterns of onset bias and nucleation probabilities (Fisher  $p < 10^{-4}$  for all subjects, statistically revealing that the onset bias and nucleation data were drawings from different distributions). See Figure 5 for the data of S2 and S4, the two subjects that participated in all experiments so far. For example, spatial segments that contain no onset bias (e.g., segment 7 in S2 and segment 3 in S4) did contain a large difference between the number of nucleations in the two eyes. Apparently, the neural factors that cause local onset bias (i.e., not being adaptation) differ from those that govern initial percept-switch nucleation. This is consistent with a claim from the literature that there is also no relationship between onset rivalry and ongoing rivalry (Carter & Cavanagh, 2007). Given that onset bias occurs without adaptation (as the images are freshly presented), and that percept-switch nucleation occurs with adaptation of one eye's image, these results reveal at least three aspects. First, these results indicate that inhomogeneous local adaptation buildup explains the difference between the results for *onset bias* and *initial percept-switch nucleation*; second, adaptation must be inhomogeneous across the visual field; and third, these results suggest that adaptation is a likely candidate to explain a large, if not the entire, portion of the nucleation probability inhomogeneity.

## Discussion

The data demonstrate that inhomogeneous patterns of eye- and observer-specific *initial percept-switch nucleations* occur for visual stimulation that is homogeneous throughout the visual field. We were able to accurately predict the inhomogeneous occurrence probability of the spontaneous nucleations on the basis of a simple “race” between spatially independent local percept-switching times measured for single stimulus elements. This suggests that the source of the *initial percept-switch nucleation* inhomogeneities occur at a relatively early, local, monocular

level of neural processing. By manipulating the duration of the stimulus in one eye that puts the system in its initial percept state, we confirmed that local monocular adaptation is a likely underlying mechanism. To constrain the range of alternative neural factors that may contribute to nucleation inhomogeneity, we compared the individual spatial patterns of nucleation probability with the corresponding patterns in onset bias, which we confirmed to be highly inhomogeneous (supporting Carter & Cavanagh, 2007). We found that such pairs of patterns are locally essentially unrelated. This excludes attributing both patterns to inhomogeneity in a common aspect of local neural processing. It is worth noting, although we did not perform a systematic experiment on a sufficient number of subjects, that the idiosyncratic distribution of nucleations remained similar across the months that we ran the experiments, consistent with the stable idiosyncratic spatial distribution of biases in onset rivalry (Carter & Cavanagh, 2007). In any case, our data make it safe to say that the similarity of nucleation distributions within one observer across the months that we ran the experiments was probabilistically larger (Fisher  $p > 0.5$ ) than the variation within distributions across observers in one experimental session.

Given that onset bias experiments do not involve unequal monocular stimulus durations (i.e., unequal adaptation) for either eye's image, our data reveal that the observed percept-switch nucleation patterns can be caused by local, random differences in adaptation properties. An adaptation-based explanation agrees with the recent finding that noisy neuronal adaptation is the driving force behind probabilistic percept duration variations, as well as their sequential correlation, in visual rivalry with continuously presented stimuli (van Ee, 2009). It also agrees with the recent finding of Alais et al. (2010) who demonstrated, using a novel sensitivity probe method, that the experienced changes during rivalry, both in suppression sensitivity and in dominance sensitivity, can be explained by neuronal adaptation. Our finding that percept-switch nucleations can be caused by local, random differences in adaptation properties may well have stayed hidden in reported “after-effect” studies because only local-scale adaptation characteristics are involved. Although nucleations in visual percept switching seem phenomenologically similar to nucleations in magnetism, adaptation buildup makes the process fundamentally different (long-range inhomogeneous binocular interaction in the cortex is another difference), thereby offering new challenges for neurophysics approaches to studying the underlying neural network dynamics.

Recent developments in optical imaging of neural activity have enabled 2D recording of traveling activity waves imposed by visual triggers at high spatiotemporal resolution (Xu, Huang, Takagaki, & Wu, 2007). It seems therefore straightforward to directly measure the more elementary process of spontaneous percept nucleation,

given that it starts at a specific location. Our findings, thus, open up new horizons for examining how well-defined perceptual experiences arise from ambiguous stimuli.

## Conclusion

We conclude that fixed, but locally random, neural characteristics that control the local percept duration underlie the eye- and observer-specific inhomogeneities in local nucleation probabilities for homogeneous stimulation. Collectively, our experiments support a governing role of local neuronal adaptation in the origination of switches in visual awareness.

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