Stochastic variations in sensory awareness are driven by noisy neuronal adaptation: evidence from serial correlations in perceptual bistability

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When the sensory system is subjected to ambiguous input, perception alternates between interpretations in a seemingly random fashion. Although neuronal noise obviously plays a role, the neural mechanism for the generation of randomness at the slow time scale of the percept durations (multiple seconds) is unresolved. Here significant nonzero serial correlations are reported in series of visual percept durations (to the author's knowledge for the first time accounting for duration impurities caused by reaction time, drift, and incomplete percepts). Serial correlations for perceptual rivalry using structure-from-motion ambiguity were smaller than for binocular rivalry using orthogonal gratings. A spectrum of computational models is considered, and it is concluded that noise in adaptation of percept-related neurons causes the serial correlations. This work bridges, in a physiologically plausible way, widely appreciated deterministic modeling and randomness in experimental observations of visual rivalry. © 2009 Optical Society of America

OCIS codes: 330.5510, 330.4060, 330.7320, 330.5020.

1. INTRODUCTION

Primate sensory perception automatically switches between alternative interpretations when there is inconclusive sensory input. Such alternations are observed clearly while the sensory system is uninterruptedly being subjected to ambiguous input, meaning that more than one mutually exclusive interpretation of the sensory input is continuously available. The alternations, which occur in hearing, touch, and vision, occur on a multiple second time scale and they seem to appear at random moments. Such a stochastic process poses the fundamental question: *Which physiological signal in the alternation process is responsible for the random percept alternations?* To answer this question we focus on alternations in *visual* awareness—a phenomenon called "visual rivalry"—where two visual percepts of an ambiguous scene compete for dominance in awareness.

The two main factors in visual rivalry are cross-inhibition [1] and self-adaptation [2] of the neuronal populations that are associated with the construction of the two percepts (review in [3,4]). Although it becomes increasingly clear that internal neuronal noise (occurring on a millisecond time scale) plays a major role in visual rivalry [5–8] the neural mechanism responsible for the generation of randomness at the slow time scale of the percept durations (multiple seconds) is unresolved.

Because of the presence of neuronal adaptation, there ought to be deterministic carryover effects across successive alternations as the neuronal adaptation modifies the beginning conditions at the next perceptual duration [2]. It is, however, not clear how a deterministic model can generate the observed stochastic behavior. A stochastic process allows for the possibility of temporal serial corre-

lation (by definition a stochastic process does not need to be completely random), meaning that serial correlations in perceptual durations may reflect footprints of the underlying deterministic perceptual alternation mechanism.

Here the role of neuronal adaptation in causing slow stochastic variation in visual awareness is studied both in experiments and in computational modeling. Our tool is the quantitative analysis of serial correlation in perceptual durations for different stimulus conditions.

A. Computational Modeling Approach

To date nonzero serial correlation in percept durations has not been employed in computational modeling. Most published models of visual rivalry employ a roughly similar interaction between self-adaptation and cross-inhibition [8–22]. Models that incorporate cross-inhibition and self-adaptation without the addition of noise would always produce equally long durations without stochastic variation (e.g., see [5,8] for a discussion of this issue) and without serial correlation. We argue that this deterministic behavior of models does actually enable us to elucidate which component of the process is responsible for serial correlation at a slow (multiple seconds) time scale. Consider the relationship between two sequential perceptual periods of either of the two competing percepts A and B. The percept duration for, say, percept B depends on the degree of adaptation of the neurons producing percept B at the moment percept B becomes dominant. This "onset adaptation value" of percept B depends, in turn, on the dominance duration of both the preceding percept B (because during dominance of percept B the adaptation of percept B increases) and the preceding competing percept A (during which the adaptation of B decays). Thus, in

models containing self-adaptation, the dominance period of a percept must depend on (i.e., correlate with) a history of the dominance periods of preceding percepts. We argue that adding white—i.e., uncorrelated—noise to a particular component of the perceptual alternation process provides a window to simulate whether that component plays a key role. Because this white noise is uncorrelated, it ought not cause serial correlations. More precisely, if serial correlations can be produced by adding white noise to the adaptation dynamics, but not by adding noise to the dynamics of the neural cross-inhibited activity, one can infer that adaptation is responsible for serial correlation.

B. Experimental Approach
In the course of decades of research only a few studies in visual rivalry have addressed serial correlation in percept duration. Fox and Herrmann pioneered [23], and ever since there have been a handful of experimental studies that reported serial correlation [24–29], of which only a few early papers focused on serial correlation in an experimental fashion [24–26]. Although all of these studies reported positive correlations the correlations were small (roughly between 0.1 and 0.2). It is obvious that the (deterministic) carryover effects across successive perceptual durations are not a major factor in the generation of percept durations. The positive correlations were regarded by the field as being too small to be taken as serious deviations from zero correlation ([9] for review). In recent years it became clear that there were a number of experimental issues that may influence perceptual duration series and that were not considered in previous determinations of serial correlation. These include

- perceptual durations exhibit slow drift over time [30–32] due to slowly changing attention, or a slow change in the number of blinks, or a variety of other sources such as, for example, long-term adaptation [33];
- data series may be impurified by piecemeal rivalry, superimposed percepts, and return-transitions to the same percept without fully experiencing the alternative percept [6,10,34];
- during the perceptual switch there is no stable perceptual state; these intermediate percepts can take up as much as 30% of the presentation duration for low-contrast stimuli [6];
- there are reaction time limitations, particularly while responding to quickly succeeding percepts.

In our experiments below these issues were taken into account. In addition two classes of stimuli were examined: gratings as a binocular rivalry stimulus and the ambiguously rotating sphere as a perceptual rivalry stimulus. For generality, we employed a parametric design in which we varied physical stimulus properties across data collection sessions (contrast for the gratings; number of dots for the sphere).

C. Aim of This Study
Below, using quantitative analysis of serial correlation in perceptual durations as a tool, model simulations of new data are employed, reported serial correlations are surveyed, and new correlation calculations of existing data are presented. We do so to investigate the role of noisy

variations in neuronal adaptation in driving stochastic variations in sensory awareness.

2. MATERIALS AND METHODS
A. Experiment 1. Binocular Rivalry, Varying Contrast
1. Apparatus and Procedure
The stimuli were presented one on either side of a gamma-corrected CRT monitor (80 Hz refresh rate) and viewed through a conventional mirror stereoscope (viewing distance 66 cm) to produce binocular rivalry. The stimulus consisted of two sine-wave gratings (±45 deg) with a diameter of 1.0 deg, and a spatial frequency of 4.0 cycles/deg on a gray background. Chin and head rests reduced head movements. To prevent drift in binocular eye posture—i.e., to keep the two eyes' gratings on top of each other, meaning that they project to corresponding retinal positions—stimuli were surrounded by unfilled squares (0.4 deg) presented binocularly. This turned out to be an important step in our experimental design in preventing piecemeal rivalry and perceptual superposition of the two eyes' gratings.

Four naïve subjects participated. First, we determined the individual threshold contrast where percept alternation was still possible, which varied from 0.10 to 0.17 Michelson. Levels were chosen along a logarithmic scale up to full contrast (1.0 Michelson), the mean luminance always being equal to the background. Each session consisted of four (five for subject S4) trial blocks, randomized for contrast (across blocks), each block comprising five min of continuous viewing, with a mandatory 2 min resting period between blocks. Each session was repeated six times, amounting to 120 min of data collection per contrast condition (150 min for S4). Subjects scored dominance of either the left or the right grating by holding down the left or right button of a computer mouse.

Our stimulus was designed to diminish both piecemeal rivalry and perceptual superposition of the two eyes' gratings for the full contrast condition, and we took advantage of the occurrence of such mixed percepts for lower contrasts. Subjects were instructed to release both mouse buttons during the occurrence of mixed percepts. For the full contrast stimulus we succeeded in diminishing the occurrence of these phenomena; within a 5 min session our subjects indicated mixed percepts for less than 5 s ($<2\%$). For the lowest contrast stimuli mixed percepts occurred frequently (up to 30%), in line with known literature [6]. The fact that there was no significant occurrence of mixed percepts for the full contrast condition means that we are looking at a pure binary percept alternation process in this condition. The occurrence of mixed percepts with lower contrasts enables us to investigate the effect of mixed percepts on serial correlations.

2. Data Analysis
To calculate serial correlation we used the Spearman rank correlation index since it is nonparametric, well-suited for our not-normally distributed data. Before a Spearman rank correlation index was calculated, the data were corrected (purified) using the following steps: (1) the first 30 s of each trial were discarded; (2) we deleted the

mixed-percept periods (so the length of the duration list was truncated); (3) a linear regression was used to probe the amount of drift in a data collection block. This drift was corrected. Although we planned on discarding the entire block from the analysis if the amount of drift in the mean percept duration was more than 0.5 s/min, the drift was always smaller. In the drift analysis we also used another frequently employed statistical method: we divided data series into smaller chunks, each of which was used to calculate the serial correlation.

B. Experiment 2. Perceptual Rivalry for the Ambiguously Rotating Sphere

This experiment was identical to experiment 1, but here we presented the ambiguously rotating sphere (4 deg diameter consisting of white dots with constant size). Our four subjects scored the perceived direction of the stimulus' front surface by holding down either the left or right button of the mouse. For ambiguous structure from motion spheres there is the possibility that subjects perceive the stimulus as two convex surfaces that are sliding on top of each other as opposed to a 3D sphere with a front and a back [35,36]. Some observers perceive the sliding-convex surfaces over 50% of the time. For others this percept hardly occurs. We selected subjects for whom this percept occurred less than 1% of the time during pretesting. We further minimized the occurrence of the percept by instructing the subject to concentrate solely on the direction of the stimulus' front surface, making the task binary and supposedly involving competition between only two neuron populations, each representing a motion direction of the front surface (gestalt) to either the right or the left [37–39]. The stimulus was presented monocularly; the nondominant eye was patched. We varied the number of dots of the sphere per session: 100, 300, 500, 700, and 900 dots. In previous work we found that there is a robust relationship between the numbers of dots on the sphere and the alternation rate [37], similar to how the alternation rate for gratings depends on the grating contrast. During each trial block subjects viewed the stimulus continuously for 5 min; there were five blocks in each session. Per subject there was a total of ten sessions, amounting to a data set of a total of 1250 min (50 min per subject per dot quantity).

C. Simulation: Noise and Serial Correlation

The two main factors in visual rivalry are self-adaptation and cross-inhibition. We first added white noise, $\delta G(\mu, \sigma)$, to the adaptation A_i of the dominant percept. As adaptation dynamics, we employed the simplest possibility: a conventional "leaky integrator" (with constant α reflecting adaptation build-up),

$$\partial_t A_i = -A_i + \alpha S[H_i] + \delta G(\mu, \sigma),$$

with δ a small scaling constant and G a standard Gaussian with peak at zero and a standard width [$G(\mu, \sigma)$; $\mu = 0$, $\sigma = 1$]. The adaptation dynamics as such is generic and conventional; it is identical in structure to the adaptation dynamics used in the models cited above. With respect to details of the adaptation dynamics, models differ slightly. To test the role of noise we selected the recent model for visual rivalry by Noest *et al.* [22] that is now supported by

a wide range of recently published phenomena and quantitative data (review in [40,41]). To be precise, the second term in the equation $\alpha S[H_i]$ is model specific by using a sigmoid function [$S(z > 0) = z^2/(1 + z^2)$; $S(z \leq 0) = 0$; i denotes one of the two alternative percepts, j the other percept]. This means that neuronal outputs occur as sigmoidal transformations $S[H_i]$ of the percept$_i$-related component of the local fields ($\sim 10^9$ neurons) that encode the two competing bistable percepts, but the precise form of the dynamics is not essential for the issues of the current paper.

The structure of the cross-inhibited neural activity dynamics equation is also conventional,

$$\tau \partial_t H_i = X_i - (1 + A_i)H_i - \gamma S[H_j];$$

it combines the standard elements, i.e., first, decaying of neural activity, and second, cross-inhibition by the other percept j in a straightforward way: The neural activity H_i integrates its visual input X_i (stimulus strength) with the gain control $(1 + A_i)$ depending on adaptation and cross-inhibition $S[H_j]$. The parameter γ is a coupling constant and τ is a time constant reflecting that cross-inhibition in this equation occurs faster than adaptation in the previous equation. For the simulations we used a fourth-order nonadaptive Runga–Kutta method [$X = 1$, $\alpha = 5$, $\gamma = 10/3$]. The parameter δ_A was 7.1, time scale separation τ was 1/30. We ran the same number of alternations as present in the experimental data to enable direct comparison. To simulate a variety of stimulus strengths (resembling contrasts or dot densities) we varied the X value from 88% up to full strength in steps of 4%.

3. RESULTS

A. Experiment 1. Significant Serial Correlation in Binocular Rivalry

We first investigated grating rivalry for our four observers. The perceptual duration distributions across the tested grating contrasts (subtending threshold to full contrast) for one typical subject (S2) are depicted in Fig. 1(a). Those distributions exhibit the often-reported characteristic long-tailed shape. From these distributions we calculated the means and the fit parameters (the scale and the shape parameters) after fitting the CDFs (cumulative distribution functions) of a gamma distribution [27,42,43] that appeared to be more suitable than other distributions. We used the CDFs for our fitting procedure because, contrary to the PDF, the CDF does not involve an arbitrary bin size. In all, we collected 520 min of data. The data lists contained at least 205 percept durations per subject per contrast condition (but usually around 400), with a total of 8861 percepts. The mean percept duration decreased with stimulus contrast (star symbols in Fig. 1(b); p < 0.05, standard regression), replicating behavioral data patterns that have been known for a long time (e.g., [44,45]). Although it is not essential for the serial correlation conclusions of this paper, note a substantiation of a relatively new insight in that modifications in both the scale parameter (star symbols in Fig. 1(c)) and the shape parameter (star symbols in Fig. 1(d)) are systematic [37,43], providing insights in addition to the obvious changes in the mean duration [43]. Although for
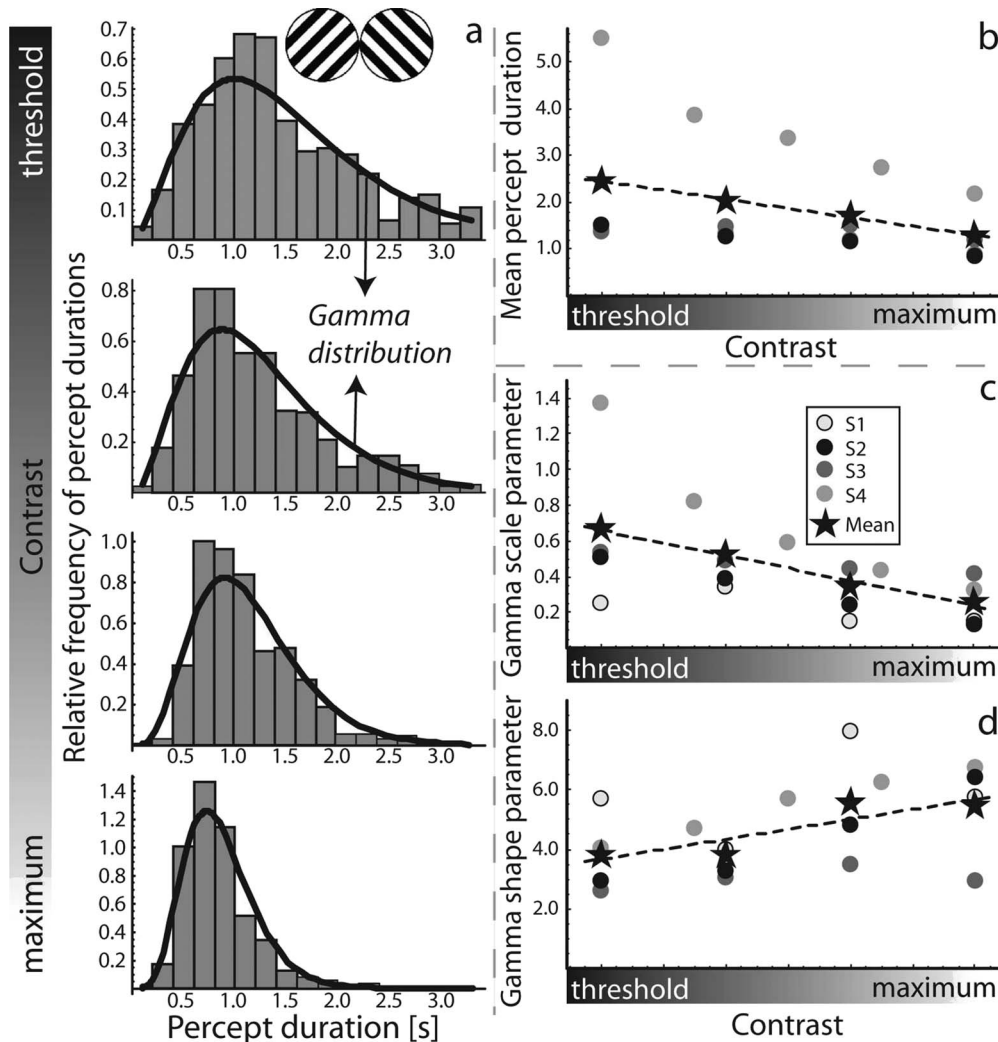
Fig. 1.   Binocular grating rivalry. a. The probability distribution of the raw percept durations of subject S2 binned (gray) and fitted by a gamma distribution (solid curve). From top to bottom grating contrast changed from threshold to maximum, producing shorter percept durations. b. Increasing the contrast entailed on average (star symbols) smaller mean durations for our four subjects. The individual subjects are denoted by disks (color online). The disks of subject S1 are covered by the disks of S2 and S3. On average, with increasing contrast, the gamma scale parameter decreases (c.) and the gamma shape parameter increases (d.). Error bars in the mean are smaller than the symbols.

subject S2 (whose individual data are displayed in Fig. 1(a)) the changes with contrast of the mean percept duration were moderate (Fig. 1(b)), S2's scale and shape parameters show a clear change with contrast (Figs. 1(c) and 1(d)). Because the mean of a gamma distribution is defined as the product of shape and scale [46], the rate of change of the scale parameter must have been larger than the rate of change of the mean duration. The variance does also decrease with contrast, as variance is defined as the product of shape and squared scale [46].

To examine serial dependence we calculated the Spearman rank correlation coefficient. Interestingly, and contrary to current thinking, the correlation of the length of a particular percept dominance period with the length of an immediately following dominance period of the same percept (denoted by lag 1) was always positive for all contrasts and all subjects (Fig. 2). Fifteen of the seventeen outcomes were significantly positive (see 95% confidence analysis below). On average the lag 1 serial correlation amounted to almost 0.2. Interestingly, given that the se-

rial correlation did not change with contrast nearly as much as the occurrence of mixed percepts did (for full contrast there was an insignificant occurrence of mixed per-
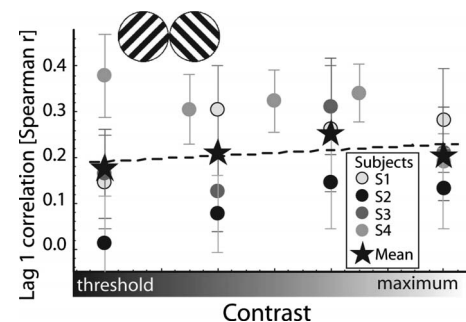

Fig. 2.   Lag 1 serial correlation for binocular grating rivalry expressed in Spearman rank correlation of (immediately) following dominance periods is always positive for all contrasts and all subjects. On average (stars) the serial correlation amounts to 0.2, i.e., 20%. Error bars, ±1 StErr.

cepts; for low contrasts mixed percepts occurred up to 30% of the time), we infer that mixed percepts do not have a clear influence on the serial correlation.

We further investigated whether the influence of a single perceptual duration extends to more than just the immediately following percept (lag 2 or more; Fig. 3). The serial correlation at lag 2 was frequently significant (9 out of 17). Significance is indicated by the dashed curves, showing the 95% significance boundaries for the baseline assumption that the correlation is zero. Those significance boundaries were calculated through computational simulations using the same number of pairs as used in the Spearman rank correlation above, meaning that they rise slightly with increasing lag (because there are fewer pairs in a list for larger lags). The boundaries depend slightly on the contrast, because the length of a list of percept durations depends on the contrast (i.e., higher contrast means more flips per minute). Although up to lag 3 all coefficients were positive, for lags greater than 2 the correlations became insignificant.

B. Reaction Time Control Experiment
Many short durations had to be reported in the experiment above, meaning that reaction time delays become an issue. Serial correlations may arise when an observer experiences a perceptual alternation that is quickly followed by the next alternation, particularly when piecemeal percepts, mixed percepts, and returns to the previous percept (without experiencing the alternative percept) also occur. A way to examine reaction time influences is to employ a "pseudorivalry" condition in which the gratings presented to the two eyes are identical, together alternating in orientation. When decision making or motor planning is responsible for the nonzero serial percept duration correla-

tion, the reported percept durations in this pseudorivalry condition should also produce nonzero correlations. We used exactly the same stimulus design as described above, except that the two eyes were presented with non-competing identical gratings. To produce a realistic pseudorivalry transition from one grating to the other grating, we incorporated superimposed gratings and incomplete transitions entailing return percepts. In 25% of the transitions the transition sequence reversed halfway, producing a return percept. Using 15 intermediate image frames during a transition, our naïve observers were not able to distinguish the fluent percept transitions produced by our pseudorivalry condition from mentally produced percept transitions. To focus on quickly following alternations, percept durations varied randomly between 0.8 and 1.4 s.

The Spearman rank correlation was calculated for both the pseudorivalry list of durations presented by the experimenter and the list of durations produced by the observer (using exactly the same analyses as described above for the previous experiment). The difference in correlation between the two data sets is the correlation produced by the observer (Table 1). The average serial correlation was 0.03 ± 0.03, not significantly different from zero, meaning that the serial percept duration correlations found in our previous experiment were not governed by imperfections in button presses.

C. Experiment 2. Significant Serial Correlation in Perceptual Rivalry
For perceptual rivalry, using the ambiguously rotating sphere, we performed exactly the same data analysis as we did above for binocular rivalry. The lag 1 correlation coefficient across the various numbers of dots on the sphere is depicted in Fig. 4. The correlation amounts to
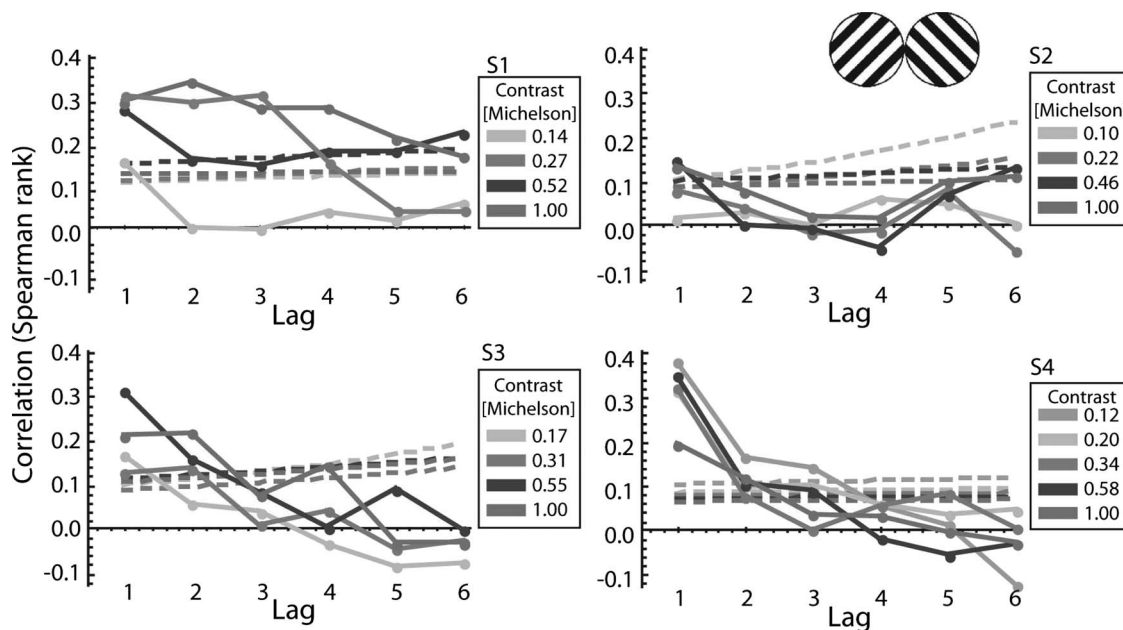

Fig. 3. Serial correlation for binocular grating rivalry expressed in Spearman rank correlation generally decreases with increasing lag number. The dashed curves specify the significance boundaries (they go up with lag because the number of data pairs used for the calculation necessarily decreases with greater lags; they depend on the contrast because the length of the data lists vary with contrast). Below those curves there is no significant correlation. The data for the immediate correlation with the next percept duration (lag 1) are replotted from Fig. 2. For lag 1 the correlation coefficient is generally significantly positive for all contrasts and all subjects. For lag 3, and also for greater lags, it is generally nonsignificant.

Table 1. Serial Perceptual Duration Correlation for the Pseudorivalry Stimuli

	Correlations (Spearman rank)				
	Blocks				
Subject	1, 2, and 3			Mean	St Dev
S1	−0.07	0.01	−0.01	−0.02	0.04
S2	0.10	0.08	0.21	0.13	0.07
S3	−0.07	0.08	0.06	0.03	0.08
S4	0.00	−0.16	0.04	−0.04	0.11
Mean		0.03±0.03			

about 0.1. Much as we found for binocular rivalry all lag 1 correlations were positive (15 out of 20 reach 95% significance), indicating that the lengths of serial durations are generally not independent. The correlation coefficients for lag 2 and higher (see Fig. 5) resemble those for binocular rivalry (Fig. 3): at lag 3 all, and at lag 2 almost all, correlations were insignificant.
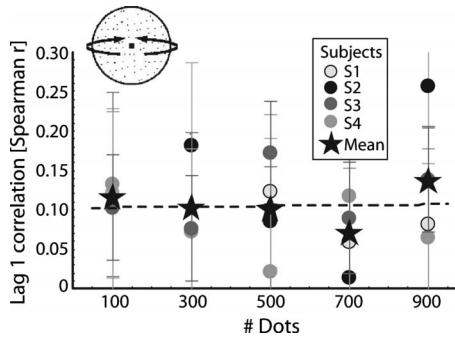

Fig. 4.   As Fig. 2 but for perceptual rivalry produced by the ambiguous sphere. The serial dependence is positive for all subjects and for the sphere's number of dots.
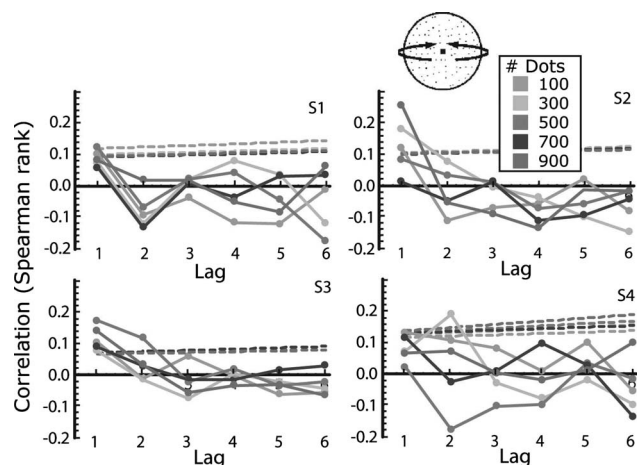

Fig. 5.   As Fig. 3 but for the ambiguous sphere containing variable number of dots. The serial correlation expressed in Spearman rank correlation generally changes with lag number. The dashed curves specify the significance boundaries. Below those curves there is no significant correlation. The data for the immediate correlation with the next percept duration (lag 1) are replotted from Fig. 4. For lag 1 the correlation coefficient is positive for all numbers of dots (significant in 10 out of 20 cases). For lag 2 and greater lags correlation is generally nonsignificant.
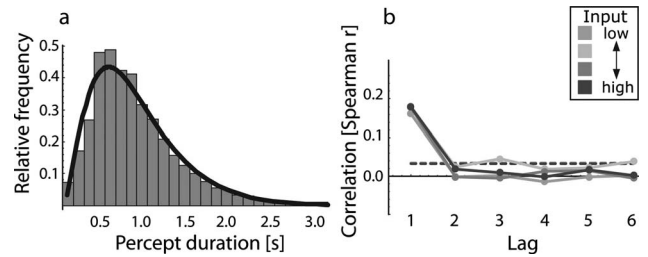

Fig. 6.   a. Percept durations (as in Fig. 1) produced by our model with white noise in the adaptation parameter (A) binned (gray) and fitted by a gamma distribution (solid curve). b. As Fig. 3 but for the model-generated percept durations. With noise in the adaptation parameter (A) the model produces positive Spearman rank correlation coefficients, particularly for lag 1. The dashed curves specify the significance boundaries (based on fixed list length). Below those curves there is no significant correlation.

D. Simulations: Noise in Adaptation Drives Serial Correlation

A typical percept duration distribution produced by the computational model employed with white noise in the adaptation dynamics (thereby covering both adaptation A and its build-up α) is depicted in Fig. 6(a). To determine serial correlation we calculated the Spearman rank correlation coefficient within the resulting list of perceptual durations, identical to what we did above for the experimentally acquired data. Figure 6(b) shows that all lag 1 correlations across the various contrasts are significantly positive. For larger lags the correlations become insignificant below the 95% significance boundaries for zero correlation. Computational modeling using multiple time scales [33] is able to produce significant higher-lag coefficients, but this goes beyond the scope of this paper.

We found that noise in the other relevant model component, the neural activity dynamics (thereby covering both activity H and cross-inhibition strength γ), was not able to account for the magnitude of the serial correlations found. The largest lag 1 correlation that we were able to produce only marginally exceeded the 95% confidence boundary (dashed line in Fig. 6(b)). Although it is obvious that the main reason for this finding is that the time scale of fast variations in cross-inhibited neural activity is rather different from the time scale of percept alternations, a limited understanding of the neural dynamics prevents us from providing quantitative graphs that facilitate unambiguous interpretation. A full understanding is lacking because all published equations on neural dynamics in perceptual bistability necessarily contain severe approximations on how to average the activity of 10^9 single neurons into one single parameter. In addition, there are multiple combinations of parameter values that lead to the same serial correlation. Thus, quantitative simulation outcomes on the role of noise in neural activity are not yet interpretable with respect to the individual parameters. In any case it seems safe to conclude that any combination of noise in the parameters associated with the neural activity dynamics does not account for the magnitude of the experimentally found serial correlations.

Noise in the stimulus strength parameter X has not been explicitly mentioned yet; Figs. 2–5 demonstrate that even large changes in the input strength hardly affect the

lag 1 serial correlations. Figure 6(b) demonstrates that the simulated lag 1 correlations are also immune to changes in the input strength (see Section 4 for consistent interpretation).

In Section 4 it is discussed that noise in neural activity actually can, via an indirect route, affect serial correlation through both the adaptation build-up of the neurons associated with the dominant percept duration and the recovery from adaptation of the neurons associated with the suppressed percept duration. It is also discussed that our approach is generic (not simply specific to the performed simulations or selected model), and that it extends a similar finding of Kim *et al.* for stochastic resonance [5] into the domain of serial correlation.

E. New Serial Correlation Analyses on Existing Attentional Control Data
To date, no studies have reported serial correlations for data series obtained under voluntary attentional control. We analysed (employing the same Spearman analysis as used above) the data series from a previously published comparison study that employed different attentional control conditions [47]. For comparison we first replotted (Fig. 7(a)) the reported serial correlations in the literature [23–29]. The pioneering Fox and Hermann (1967) [23] data are not in this plot because it did not report lag 1 correlations, only higher-lag correlations. We have also published serial correlations in a paper that explored in detail the differences in dynamics for four different rivalry stimuli under identical stimulus presentation conditions. Our data, too, contained unanimous positive lag 1 correlations for all stimuli [31], here replotted in Fig. 7(b), left panel.

The previously published comparison study [47] of which we now analyze the produced serial correlations was based on 60,000 perceptual reversals for four different rivalry stimuli under different attentional voluntary control tasks. The tasks involved either holding one of the

two percepts in dominance or viewing the stimulus in a passive way without exerting attentional control. Interestingly, for the more cognitive stimuli (for example, slant rivalry involving highly cognitive interpretation of linear perspective) and for the higher-level cognitive task (hold a percept in dominance) the serial correlations tend to become smaller (Fig. 7(b), right panel). Figure 7(c) demonstrates that the lag 1 serial correlation for the *passive* task correlates (negatively) with the effectiveness of voluntary control in lengthening the perceptual duration (for the *hold* task relative to the *passive* task). For the more cognitive stimuli, where top-down voluntary attentional control exerts more influence, there is a smaller lag 1 correlation, suggesting that the perceptual alternation process is less prone to noisy variations in the neuronal adaptation associated with percept dominance.

4. DISCUSSION
Using a computational analysis based on straightforward theoretical principles, it is demonstrated that noise in adaptation of percept-related neurons can cause the observed slow stochastic variations in sensory awareness on a multiple seconds time scale. In addition, evidence is provided that serial correlations depend on stimulus and task. This work forms a means of bringing together, in a physiologically plausible way, widely appreciated deterministic modeling and the randomness component in experimental observations in visual rivalry. Although we confirm previous literature ([9] for review) to the extent that carryover effects across successive perceptual durations are not the major factor in the generation of percept durations, we found significant serial correlation of pure perceptual durations (accounting for impurities caused by reaction time, drift, and incomplete percepts) in both binocular and perceptual rivalry. This contradicts a frequently occurring idea among scientists in the field that complete randomness of perceptual periods constitutes a hallmark of visual rivalry. Although we focused on the visual domain, from emerging evidence in other sensory domains ([48,49] for audition, and [50] for touch) it appears that the dynamics of series of perceptual dominance durations are strikingly similar across the sensory domains, implying that our findings may be extended to other sensory domains.

A. Neuronal Noise at a Slow Time Scale of Percept Adaptation
It is remarkable, but also revealing, that our computational simulations produce correlated serial perceptual durations by adding white (i.e., uncorrelated) noise that ought not cause the serial correlations. Recently it became increasingly clear that noise must play a major explaining role [5–8], but the neural mechanism responsible for the generation of stochastic behavior at the slow time scale of percept durations remained unresolved. We reasoned that adding noise to a particular component of the competition process provides a window to simulate whether it plays a key role in the process. We found, on one hand, that noise in the slow adaptation dynamics was able to account for the experimental data patterns (Fig. 6(b)). On the other hand, noise in the dynamics of cross-
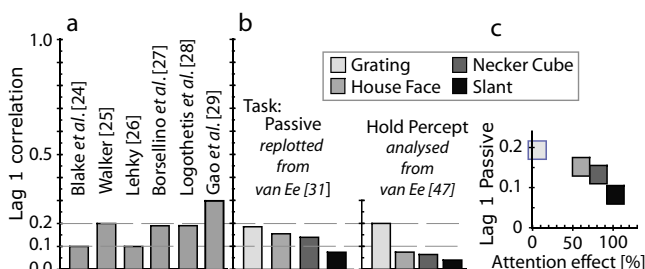

Fig. 7.   a. Data from other laboratories. b. Previous data from our own laboratory. It is obvious that serial correlation is generally positive irrespective of task and stimulus. Interestingly, for the more cognitive stimuli (slant rivalry) and for the higher-level task (hold) the serial correlations tend to become smaller. c. The lag 1 serial correlation for the passive task correlates negatively with the percentage of voluntary control in lengthening the perceptual duration (for the hold task relative to the passive task). For the gratings there is a small effect of voluntary control and there is a considerable lag 1 correlation for the passive task. For the more cognitive stimuli, where the conscious act of voluntary control has more influence, there is a smaller lag 1 correlation for the passive task. These data support the speculation that a more cognitive task produces less lag 1 serial correlation in perceptual duration, i.e., the alternation process is then less prone to internal variation in neural adaptation.

inhibited neural activity was not able to account for the magnitude of serial correlations found. Note that even large changes in the input strength hardly affected either the experimentally found or the simulated serial correlations (Figs. 2–6). These findings nicely dovetail with the interpretation that serial correlation is governed by variation in adaptation of percept-related (as opposed to stimulus-related) neurons.

Why is it that noise in the parameter associated with neural activity *per se* does not produce the serial correlations found? For one thing, cross-inhibition is physiologically a key element in the competition process [1], which naturally contains (Poisson) noise in the neuronal firing patterns. However, the time scale of fast variations in cross-inhibited neural activity is rather shorter than the time scale of percept alternations: while the percept strength slowly changes from being suppressed to being dominant, the neural activity noise produces rapid random jittering on those percept strengths. Close to the deterministic alternation moment this noisy jittering can make the perceptual alternation happen more quickly or more slowly. The same is true for the next alternation where the noise will determine another random variation in the alternation moment, which is unrelated (i.e., uncorrelated) to the first. Thus, noise in neural activity *per se* is unable to cause directly the serial correlations found.

However, by producing jittering in percept durations this noise will indirectly affect both the adaptation build-up of the neurons associated with the dominant percept duration and the recovery from adaptation of the neurons associated with the suppressed percept duration. This implies that noise in neural activity can produce marginal serial percept duration correlations indirectly through adaptation, bringing us back to our computational finding that variations in adaptation account for the experimentally found pattern of serial correlations. This reasoning is supported by literature on stochastic resonance [5] (see below) and we argue that it holds in a general sense.

B. How Generic is Our Finding?
How generic is our finding—that serial correlations are caused by variations in the slow time scale of neural adaptation—and how specific is it to the simulations performed (using the Noest-2007 model)? We considered various classes of models. The grand class of models, including the model we used, involves interaction between adaptation and cross-inhibition [8–10,14–21]. All these models behave in a similar way under noise in the adaptation component, meaning that our finding applies to a broad class of models. Note that a similar claim can be found in the literature for stochastic resonance. Kim *et al.* (2006) [5] explicitly compared a number of influential adaptation models and also found that adding noise to adaptation, rather than to neural activity, was crucial in producing the stochastic resonance that they obtained experimentally.

Other classes of models involve random walks [51,52], Markov chains [53], or random fractal theory [54]. These are interesting and inspiring from a theoretical point of view, but they await physiological implementation. Until then it is impossible to state which model parameter would be responsible for serial correlation in human behavioral data. Other models, some very recent, that use multiple layers [55–57], multiple neuron pools [58], or oscillator coding [59] cannot be generic models because they do not explain now-established experimental findings on multiple time scales in perceptual memory ([40,41] for review) and/or experimental findings that led to the modification of Levelt's second proposition [6]. It is often assumed that all models produce long-tailed (gamma or lognormal) percept duration distributions, but there is a class of statistical models that does not [60], thereby failing to fit experimentally found percept duration distributions.

There is one paper, by Gao *et al.* [29], that is seminal in presenting a model producing positive serial correlations, supporting experimentally obtained correlations of as large as 0.3, which are published in the same paper. Their model provided an explanation for this correlation based on an $1/f$ analysis. However, $1/f$ analyses are very sensitive to drift in the data, and this study did not consider drift. Given the serial correlation they found of as much as 0.3 and their long periods of observation (5 min), it may be suspected that their substantial correlation was simply caused by drift and could therefore be explained by $1/f$ noise. These authors validated their theoretical findings with the huge memory effects reported for perceptual stabilization in onset rivalry after intermittent blank periods [61], thereby confusing serial correlation in switches under prolonged viewing (a switch process involving negative cross-inhibition) with perceptual stabilization in onset rivalry (a choice process involving positive priming [22]; review in Pearson and Brascamp [40]).

C. Possible Flaws in Experimentation
There are reasons to expect positive correlations between successive durations due to mechanisms not related to the stochasticity issue. For example, a gradual change of attention (either focusing, or diverting [62]) and/or the number of blinks can cause positive serial correlation. Our drift correction takes care of a gradual change over the 5 min observation period. Short-term changes in attention or blink rate may be responsible for the deviations from the mean values in Fig. 2 and Fig. 4. However, it is clear that we find quite constant lag 1 serial correlations across varying stimulus contrast for the grating (Fig. 2) and across the number of stimulus elements for the ambiguously rotating sphere (Fig. 4). This would then mean that the number of blinks did not change considerably across the different stimulus presentation blocks. One would expect more blinks and eye movements with increasing stimulus ambiguity such as one experiences when there are many mixed percepts for low-contrast gratings. However, even then we found quite constant serial correlations (Fig. 2). In addition to different stimuli, we examined different attentional states, finding that for the grating the serial correlation did not change across attentional tasks (Fig. 7(b)). Thorough eye movement studies, in which we measured microsaccades and blinks [63–65], did not reveal gradual changes over time in the amount of blinks and microsaccades.

Serial correlations were smaller for the ambiguously rotating sphere (Fig. 4) than for the grating stimulus (Fig.

2). A first explanation, but an incorrect one, would be that mixed percepts (both piecemeal rivalry and intermediate percepts of superimposed gratings) occurring for the grating stimulus but not for the ambiguously rotating sphere cause the larger correlation coefficients. This cannot be the case because for the high-contrast gratings mixed percepts did not occur to any significant extent ($<2\%$). Instead, the fact that we found very similar (Fig. 2) serial correlations both for high grating contrast (no mixed) and low grating contrast (many mixed percepts) enables us to conclude that mixed percepts do not influence serial correlations to a great extent.

D. Binocular Rivalry versus Perceptual Rivalry

It is interesting to further discuss the differences between binocular and perceptual rivalry: Although computational principles just prior to the production of visual awareness appear to be common to the two types of rivalry [66,67], the neuronal input to the computational mechanism of rivalry must stem from different cortical neurons and different cognitive levels. Indeed, the differences found in serial correlation may point to qualitatively different underlying mechanisms for binocular and perceptual rivalry, a suggestion that has been made before [31,39,47,65,68]. Meng and Tong [68] as well as van Ee *et al.* [47] recognized that top-down attentional control is more effective for perceptual rivalry than for binocular rivalry. Van Ee [31] demonstrated that the temporal dynamics are different for binocular and perceptual rivalry, and we also showed that eye movements (including microsaccades) play a larger causal role for percept-switching in binocular rivalry than in perceptual rivalry [65]. It may be the case that the difference in serial correlation indicates that for perceptual rivalry of the ambiguous sphere the two (high-level) surface gestalt interpretations rival [37–39,66], while in grating rivalry both the (high-level) grating gestalts but also the lowest-level line detectors rival, thereby producing more noisy variation in neuronal adaptation and thus more serial correlation. In a similar vein, we speculate that serial correlation produced during high-level attentional control tasks (like holding the percept) tend to be smaller (i.e., less prone to internal noisy variation in neuronal adaptation) than those produced under passive viewing (Fig. 7). It is noteworthy that, consistent with our findings, a previous study by Richards *et al.* [69] reported that the dynamics of perceptual bistability is more "structured" in the sense of deterministic chaos (i.e., less dependent on noisy variation in adaptation) for perceptual rivalry than for binocular rivalry. Future data and analyses for different "cognitive tasks" may challenge the speculations from this paragraph.

E. Findings Supporting Nonrandomness in Percept Durations

Besides our findings and the findings from the studies in Fig. 7, there are other indications that the visual rivalry process may not produce purely randomly occurring perceptual alternations. A previous study reported that perceptual durations produced by visual rivalry exhibits low-dimensionality characteristics associated with a deterministic nonlinear dynamical system showing chaotic behavior (chaotic meaning deterministic with unpre-

dictable future) [69]. A related study by Lehky [26] performed two tests for a chaotic perceptual duration generator: in the first test, a *correlation dimension test*, it was reported that correlation dimensions as a function of embedding dimension (involving time delay) deviated from what would have been found on the one hand for a chaotic generator (up to embedding dimension of 10), and on the other hand it deviated from what would have been found for a true random generator; in the second test, a *nonlinear forecasting test*, it was reported that perceptual duration series were more predictable than randomized surrogate data by about 5% (significant by $\approx 1-2$ sigmas). Nevertheless, these findings were regarded by the field as being too small to be taken as serious deviations from zero correlation, and zero correlation remained a hallmark of visual rivalry ([9] for review).

A relevant paper by Mamassian and Goutcher (2005) on temporal rivalry dynamics showed that survival probabilities of binary percepts are not random [30]. Findings on perceptual trapping in which one sequence of percepts in multistability is more likely than another sequence [70] indicate that high-level gestalt grouping of stimulus features are important in determining successive percepts. Other findings on the role of mood and attentional control in modifying perceptual durations [71] provided indications, too, that the visual rivalry process does not produce purely random percept durations. These latter findings relate to the discussion above on top-down influences.

F. Zero Serial Correlation of Percept Durations is Not a Hallmark of Visual Rivalry

Our data counteract a previous "Poisson clock" model [46] that predicts purely random uncorrelated percept durations. Historically, it was quickly recognized that percept duration distributions had a characteristic long tail that was reasonably well fit by a gamma distribution [46]. Such a distribution can theoretically be produced by a process involving a Poisson clock. Relevant here is that such a random clock, in turn, appears to generate serially uncorrelated perceptual durations. Given that the first study on serial correlation concluded that correlation was zero [23], initially there seemed to be clear evidence that a Poisson clock must underlie awareness alternations in visual rivalry [46]. Relevant recent work by Murata *et al.* provided a new angle to this issue as it reported quantized perceptual duration distribution fit parameters for different ambiguous stimuli that support the Poisson clock model [72]. In our work, however, we were not able to replicate their findings because of our study's statistical power, and we noted that the results of their study may lack convincing statistical power as well [42]. Nevertheless, it would be interesting to pursue such experiments in more detail because such results might challenge current model predictions.

Zero correlation of serially consecutive perceptual periods is frequently used as a hallmark of visual rivalry, and this idea has exerted a considerable influence on the route followed by theorists as it has often been used as a constraining boundary condition in the design of mechanistic models of visual rivalry. A stochastic process is a random process that allows serial correlation, meaning that with

regard to the random component there is nothing detrimental in accepting that serial correlations are nonzero. Note that in the literature there is not one single experiment that produced zero serial correlations, and that our significance analyses support nonzero correlation as well. All reported experimental outcomes on serial correlation are in excellent agreement with our outcomes. Even though findings from the literature could equally well have been used to criticize a sole contribution of a random switch generator, they instead were used as support for the Poisson clock model. Given the above reviewed work on a deterministic component as well as on a role of higher-level attentional effects in the alternation process, it is harder to explain away the nonzero serial correlations than to accept them as reflecting a deterministic component to the alternation process. This is even more the case when realizing that, on the one hand, the neuronal mechanism responsible for the generation of pure randomness at a time scale of percept durations is unresolved, while on the other hand there is straightforward neural modeling [22] that is consistent with a wide range of findings and that naturally produces serial correlations of a magnitude that matches experimentally found correlations.

5. CONCLUSION

Significant nonzero serial correlation in perceptual durations are reported, and evidence that serial correlations depend on stimulus and task is provided. Developing a nonspecific computational logic based on straightforward theoretical principles, it is demonstrated that noise in adaptation of percept-related neurons can cause the observed slow stochastic variations in sensory awareness on a multiple seconds time scale. This work bridges, in a physiologically plausible way, discrepancies between widely appreciated deterministic modeling and randomness in experimental observations in visual rivalry.

ACKNOWLEDGMENTS

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