

Cumulative history quantifies the role of neural adaptation in multistable perception

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Neural adaptation plays an important role in multistable perception, but its effects are difficult to discern in sequences of perceptual reversals. Investigating the multistable appearance of kinetic depth and binocular rivalry displays, we introduce *cumulative history* as a novel statistical measure of adaptive state. We show that *cumulative history*—an integral of past perceptual states, weighted toward the most recent states—significantly and consistently correlates with future dominance durations: the larger the *cumulative history* measure, the shorter are future dominance times, revealing a robust effect of neural adaptation. The characteristic time scale of *cumulative history*, which may be computed by Monte Carlo methods, correlates with average dominance durations, as expected for a measure of neural adaptation. When the *cumulative histories* of two competing percepts are balanced, perceptual reversals take longer and their outcome becomes random, demonstrating that perceptual reversals are fluctuation-driven in the absence of adaptational bias. Our findings quantify the role of neural adaptation in multistable perception, which accounts for approximately 10% of the variability of reversal timing.

Keywords: binocular vision, perceptual organization, temporal vision

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Introduction

When we view an ambiguous display, its visual appearance continues to fluctuate between two or more alternative states (Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Sterzer, Kleinschmidt, & Rees, 2009). Several factors are thought to contribute to the temporal evolution of such “multistable percepts”: first, the neural representations of alternative appearances inhibit each other, so that exactly one appearance dominates at any moment (Alais, Cass, O’Shea, & Blake, 2010; Blake, Westendorf, & Fox, 1990). Second, neural adaptation progressively destabilizes the currently dominant appearance, limiting its duration (Kang & Blake, 2010; Nawrot & Blake, 1989; Petersik, 2002; Wolfe, 1984). Third, stochastic fluctuations of neural activity initiate reversals at irregular intervals (Brascamp, van Ee, Noest, Jacobs, & van Den Berg, 2006; Hollins, 1980; Kim, Grabowecky, & Suzuki, 2006). Fourth, volitional processes, such as eye movements, eye blinks, or attention shifts, may also trigger reversals of appearance (Leopold, Wilke, Maier, & Logothetis, 2002; Mitchell, Stoner, & Reynolds, 2004; van Dam & van Ee, 2006, but see Pastukhov & Braun, 2007).

A causal role of neural adaptation in multistable perception predicts that dominance durations should depend on prior dominance history, such that particularly long periods of dominance of a particular percept should

be followed by particularly short periods of the same percept, and *vice versa*. However, numerous studies have failed to find such negative correlations between past and future dominance periods (Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972; Fox & Herrmann, 1967; Lehky, 1995; Walker, 1975). Instead, sequential correlations between dominance periods are typically weak and only significant for some displays (van Ee, 2009). Indeed, the most compelling evidence for a history dependence of multistable perception was obtained after adaptation to non-ambiguous displays and not from the normal multistable dynamics (Blake et al., 1990; Nawrot & Blake, 1989; Petersik, 2002; Wolfe, 1984).

In particular, prolonged viewing of a non-ambiguous stimulus leads to the dominance of the opposite appearance in a subsequent ambiguous display (Nawrot & Blake, 1989; Petersik, 2002; Wolfe, 1984). Similarly, when the dominance of one percept is forced (by physical perturbation), its subsequent dominance periods are unusually short and those of the other percept unusually long (Blake et al., 1990), implying that prior dominance of a percept mitigates against its future dominance. When the contrasts of competing percepts are modulated randomly and the average modulation leading to a reversal is reconstructed, prolonged periods of increased contrast (and, thus, of adaptation) are found to precede reversals (Lankheet, 2006). More recently, Kang and Blake (2010) blended non-ambiguous adaptation into the normal reversal sequence of an ambiguous (binocular rivalry) display,

by means of removing the suppressed stimulus during some dominance periods. Their results confirmed that prolonged adaptation increases the probability of reversals. Finally, Alais et al. (2010) examined visual sensitivity during the continuous viewing of a physically unchanged, multi-stable display. Toward the latter part of dominance periods, visual sensitivity decreased slightly, consistent with selective adaptation to the dominant percept.

In summary, although neural adaptation undoubtedly contributes to multistable perception, it has been difficult to discern this contribution in the normal reversal sequence of a continuously viewed, ambiguous display. To fill this gap, we here introduce *cumulative history* (an integral of past perceptual states, weighted toward the most recent states) as a novel and more sensitive measure of adaptive states during multistable perception. With this measure, linear correlations between past history and future dominance durations are consistently significant and approximately twice as large as with conventional measures. We also extract from reversal sequences the characteristic time constant of *cumulative history*. Finally, we show evidence that perceptual transitions are driven by stochastic fluctuations when the adaptive states (as measured by *cumulative history*) of competing percepts are balanced.

Methods

Observers

Sixteen observers (10 females, 6 males, including author AP) with normal or corrected-to-normal vision participated in two experiments: kinetic depth (KD) and binocular rivalry (BR). Procedures were approved by the Medical Ethics Board of the Otto-von-Guericke-Universität, Magdeburg, and informed consent was obtained from all observers. Apart from AP, all observers were naive to the purpose of the experiment and were paid to participate.

Apparatus and stimuli

Stimuli were generated in real time (HP xw8000 PC, <http://www.hp.com>) and displayed on a 19" CRT screen (Iiyama Vision Master Pro 454, <http://www.iiyama.com>), with a spatial resolution of 1600×1200 pixels and a refresh rate of 100 Hz. The viewing distance was 95 cm, so that each pixel subtended approximately 0.011° . Background luminance was 26 cd/m^2 for the kinetic depth and 19 cd/m^2 for the binocular rivalry displays. Anaglyph glasses (red/cyan) were used for the dichoptic presentation.

The kinetic depth effect stimulus (KD, Figure 1A and Movie 1) consisted of an orthographic projection of 300 dots distributed on a sphere surface (radius of 3°). Each dot was a circular patch with a Gaussian luminance profile ($\sigma = 0.057^\circ$) and a maximal luminance of 63 cd/m^2 . The sphere was centered at fixation and rotated around

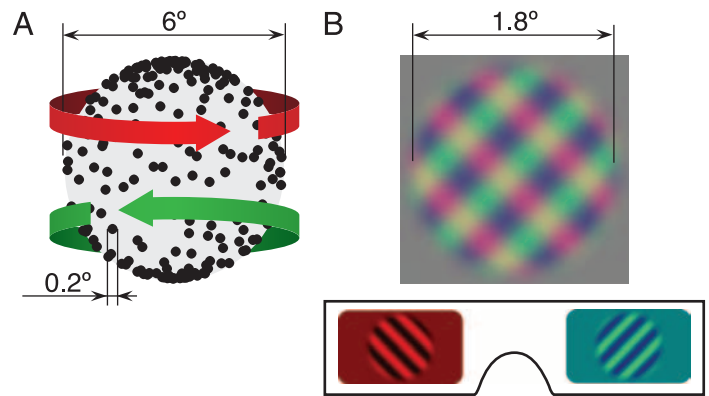


Figure 1. Multistable displays used in the study. (A) Observers view the two-dimensional projection of a rotating cloud of dots: Phenomenally, they experience rotation in depth, with the front part moving at times to the left and at times to the right (“kinetic depth”, KD). (B) With each eye, observers view a grating of different color and orientation: Their visual experience is dominated at times by one grating and at times by the other (“binocular rivalry”, BR). Less often, a patchwork of red and green areas is experienced as well.

the vertical axis with a period of 4 s. As front and rear surface dots were indistinguishable, the orthographic projection was perfectly ambiguous and consistent with either a clockwise or a counterclockwise rotation around the axis. Observers perceive a three-dimensional sphere, which reverses its direction of rotation from time to time.

The binocular rivalry stimulus (BR, Figure 1B) consisted of two gratings presented dichoptically at fixation (radius of 0.9° and spatial frequency of 2 cycles/deg). One grating was tilted leftward by 45° and the other rightward by 45° . The right-eye grating (green, visible only through the green filter) was kept at 50% contrast, while the contrast of the left-eye grating (red, visible only through the red filter) was adjusted for each subject to balance perceptual strengths. Binocular rivalry gives rise to several alternative perceptual states: two uniform percepts of either the left- or right-eye grating as well as different kinds of transitional percepts. Transitional percepts may be “fused” (i.e., both gratings are perceived) and/or “fragmented” (i.e., parts of both gratings are perceived in different image regions).

Procedure

Observers viewed the display continuously and reported the presence and identity of a clear and uniform percept. Observers pressed either the \leftarrow key (for left rotation or left-eye [red] grating), the \rightarrow key (for right rotation or right-eye [green] grating), or \downarrow key (for mixed or patchy percepts). Each presentation lasted for 5 min, separated by a compulsory break of (at least) 1 min. Consistent with previous reports (Lehky, 1995; Mamassian & Goutcher,

2005), reversal rates slowed during the initial part of the block, so that only the last 4 min (minus the final, incomplete dominance period) of each presentation were analyzed. Total observation time was 60 min (12 blocks) per observer for KD and 90 min (18 blocks) per observer for BR stimulus. Average number of clear percepts per block was 36 for KD and 110 for BR.

Statistical analysis

From the sequence of dominance periods T_i , we computed the mean dominance time, coefficient of variation, and autocorrelation as

$$T_{\text{dom}} = \frac{1}{N} \sum_{i=1}^N T_i, \quad C_v = \frac{\sqrt{\sum_{i=1}^N (T_i - T_{\text{dom}})^2}}{\sum_{i=1}^N T_i},$$

$$c_T = \frac{\sum_{i=1}^N (T_i - \langle T_i \rangle)(T_{i+1} - \langle T_{i+1} \rangle)}{\sigma_{T_i} \sigma_{T_{i+1}}}. \quad (1)$$

Standard errors (as shown in Figure 4) were obtained with a Monte Carlo procedure. From each full set of dominance

periods, 1000 random subsets were independently drawn, each comprising 75% of the dominance periods. For every subset, the mean dominance time (T_{dom}), the coefficient of variation (C_v), and the autocorrelation (c_T) were computed. The standard error for each statistical measure was then computed as the standard deviation across the 1000 bootstrapped values.

After analyzing each presentation separately, the final values for the mean and standard error of T_{dom} , C_v , and c_T were obtained by averaging the appropriate values over all presentations.

To quantify the cumulative influence of earlier perceptual experience, we introduced a measure of *cumulative history*, $H_x(t)$ (see Figure 2). Let $S_x(t)$ be a record of perceptual experience x as a function of time t , defined as unity while percept x dominates, 0.5 during a mixed or patchy percept, and zero when percept x is suppressed. The cumulative history $H_x(t)$ computed using a leaky integrator (Tuckwell, 2006) is then given by

$$\tau_H \frac{dH_x}{dt} = -H_x(t) + S_x(t) \Leftrightarrow H_x(t) = \frac{1}{\tau_H} \int_0^t S_x(t') \exp\left[-\frac{(t-t')}{\tau_H}\right] dt', \quad (2)$$

where τ_H is a time constant to be determined empirically. This definition assumes that (i) the contribution of past

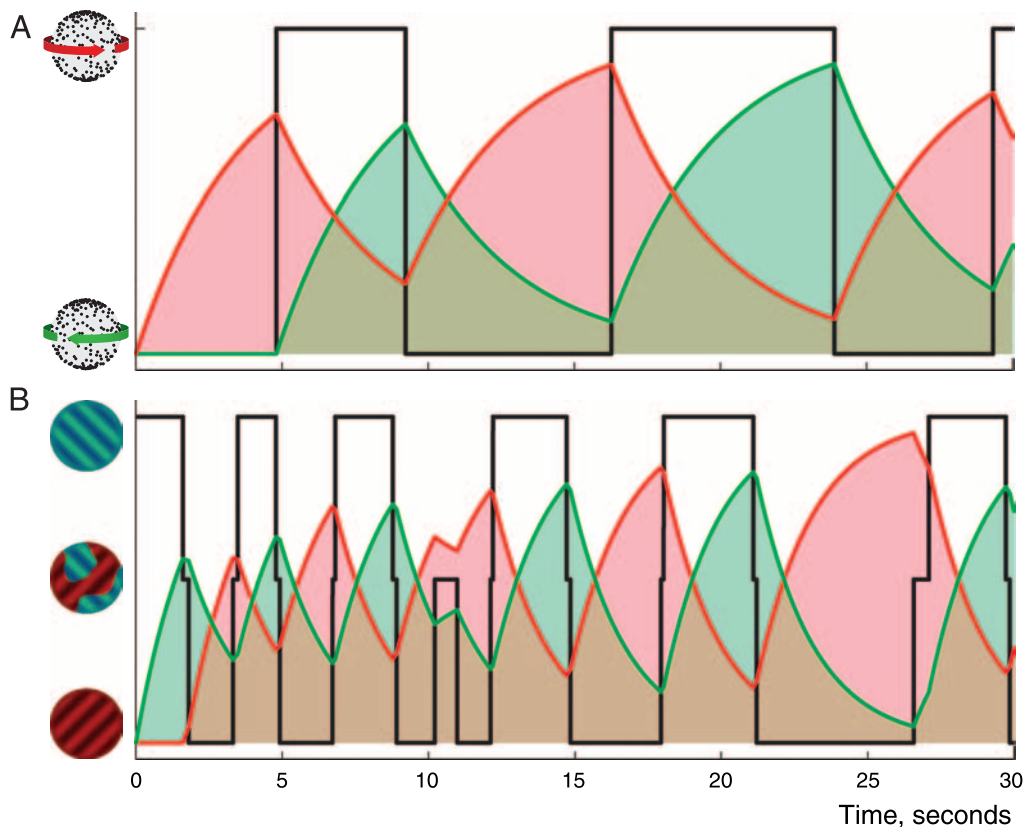


Figure 2. Example of cumulative history traces for series of reversals of visual appearances. (A) KD and (B) BR displays. The black traces indicate the reported visual appearance (“left” or “right” for KD; “green,” “red,” or “patchy” for BR). The colored traces illustrate hypothetical *cumulative histories*, computed with $\tau_H = 0.5T_{\text{dom}}$ (see text for details).

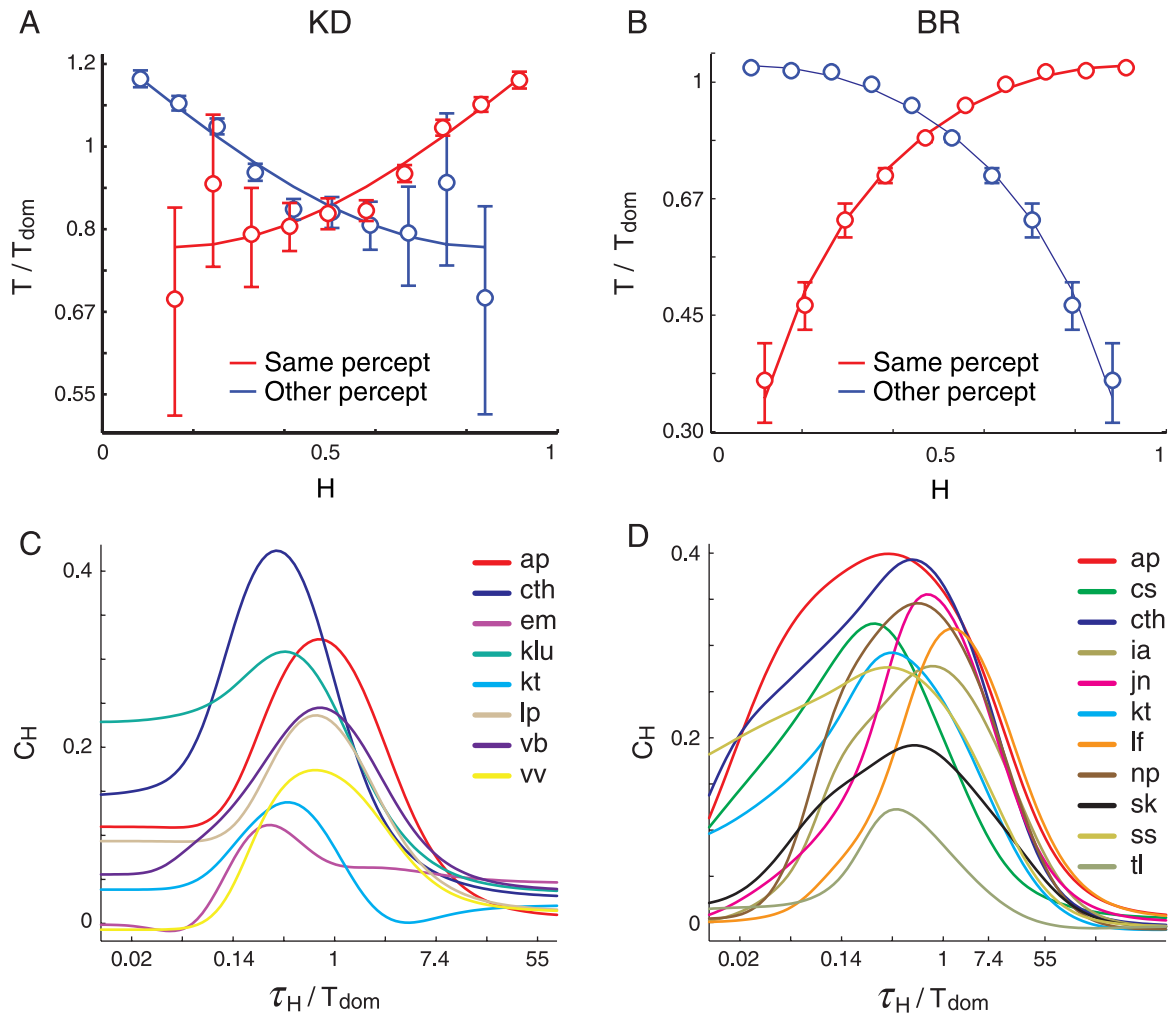


Figure 3. Individual dominance periods depend on dominance history. (A, B) Dominance periods T of one percept (normalized mean \pm standard error in bins of $\Delta H = 0.1$), as a function of the cumulative history H of the same (red), or other (blue), percept, at the time of the initial reversal. Note that $H_{\text{same}} + H_{\text{other}} \approx 1$. (C, D) Pearson correlation coefficients c_H (mean absolute values) between dominance duration and history, as a function of the decay constant τ_H . The colors identify different observers (see inset). The maximal correlation is obtained for values of $\tau_H \approx 0.5T_{\text{dom}}$.

experience decays exponentially, (ii) multiple contributions of the same percept combine additively, and (iii) there is no contribution (not even a negative one) from competing percepts.

After computing the cumulative histories H_l and H_r for two alternative percepts (e.g., left- or rightward rotation, left- or right-eye grating) from a sequence of dominance periods up to time t , we computed linear correlation coefficients with the immediately following dominance period T^l or T^r . Specifically, if t_i marks the beginning of dominance period T_i^x , we computed linear correlations between $H_x(t_i)$ and $\ln(T_i^x)$ for all four possible combinations of history and percept ($H_l \times T^l$, $H_l \times T^r$, $H_r \times T^r$, and $H_r \times T^l$). The resulting four values were then combined into an average absolute correlation.

To determine the characteristic time constant for each presentation, we performed a linear regression on the

series of dominance times T_i and obtained the residual (“detrended”) values. This ensured that $c_H \rightarrow 0$ as $\tau_H \rightarrow \infty$. Next, we used the “detrended” T_i to compute average absolute correlations for values of τ_H ranging from 0.001 s to 60 s. The maximal correlation obtained was taken as the value of c_H , and the τ_H yielding this maximal correlation was taken as the definitive value of τ_H (see Figure 3).

After analyzing each presentation separately, the final values for the mean and standard error of c_H and τ_H were obtained by averaging the appropriate values over all presentations.

The fraction of the variance of dominance periods $\text{Var}(\ln T)$ that is explained by cumulative history may be defined with respect to the linear regression:

$$\ln T = \alpha H + \beta, \quad (3)$$

and computed as the coefficient of determination R^2 :

$$R^2 = 1 - \frac{\text{Var}(\ln T - \alpha H - \beta)}{\text{Var}(\ln T)} = c_H^2. \quad (4)$$

Mutual information was computed by discretizing dominance times $\ln T$ (bin width of 300 ms) and *cumulative history* H (bin width of 0.05) and by comparing the joint distribution $P(\ln T, H)$ with the marginal distributions $P(\ln T)$ and $P(H)$:

$$I_m = \sum_{\ln T, H}^n P(\ln T, H) \log_2 \frac{P(\ln T, H)}{P(\ln T)P(H)}. \quad (5)$$

Results

We studied two canonical, but quite different, kinds of multistable displays (Figure 1A and Movie 1): kinetic depth (KD) in a two-dimensional projection of a rotating cloud of dots (Wallach & O’Connell, 1953) and binocular rivalry (BR) between two gratings of different color and orientation (Meng & Tong, 2004; Wheatstone, 1838). Eight observers viewed the KD display continuously for 5 min and reported its apparent rotation in depth as either “front left” or “front right.” The BR display was viewed for the same period by eleven observers, who reported its appearance as either “uniformly red,” “uniformly green,” or “patchy” (i.e., a patchwork of red and green areas). Spontaneous reversals of appearance occurred with both displays but were less frequent with the KD displays: The average dominance duration of uniform appearances was $T_{\text{dom}} = 11.4 \pm 7.6$ s for KD and $T_{\text{dom}} = 2.5 \pm 1.05$ s for BR. The patchy appearance (only BR) lasted for 1.05 ± 0.42 s on average.

As is typical for multistable percepts (Borsellino et al., 1972; Fox & Herrmann, 1967; Walker, 1975), dominance periods were highly variable, approximately Gamma-distributed and were shorter during the initial part of the block (Lehky, 1995; Mamassian & Goutcher, 2005). The coefficients of variation were $C_v = 0.67 \pm 0.18$ (KD) and $C_v = 0.48 \pm 0.12$ (BR). Correlations between successive dominance periods of the same appearance were fairly small ($c_T = 0.09 \pm 0.1$ for KD and $c_T = 0.15 \pm 0.05$ for BR) and reached significance ($p < 0.05$) for one (of 8) observer of the KD display and for four (of 11) observers of the BR display. Because sequential correlations are weak and often fail to reach significance, multistable perception has sometimes been considered a “memoryless” process (Blake, Fox, & McIntyre, 1971; Borsellino et al., 1972; Fox & Herrmann, 1967; Leopold & Logothetis, 1999; Levelt, 1965; Walker, 1975).

Contrary to this view, dominance times do reflect past perceptual history in subtle but consistently significant ways. To demonstrate this, we compute hypothetical states of selective adaptation for each percept, which we term *cumulative histories*. Specifically, we convolve the record of dominance reports, $S_x(t)$ with an exponential kernel (Drew & Abbott, 2006; Tuckwell, 2006) to obtain a cumulative measure of perceptual history up to time t :

$$H_x(t) \approx \frac{1}{\tau_H} \int_0^t S_x(t') \exp\left[-\frac{(t-t')}{\tau_H}\right] dt', \quad (6)$$

where $x \in \{\text{right/left, red/green}\}$ denotes a uniform percept and τ_H is a time constant. $S_x(t)$ takes values of 1 for dominance, 0.5 for patchy dominance (BR only), and 0 for non-dominance. The cumulative history $H_x(t)$ reflects both how long and how recently a given percept has dominated in the past. Figure 2 illustrates the time courses of $S_x(t)$ and $H_x(t)$, for two representative series of dominance reports. Note that, in the absence of “patchy” appearances, for example, for KD stimulus, the cumulative histories of two competing percepts approach unity ($H_{\text{left}} + H_{\text{right}} \approx 1$).

For suitable values of τ_H (see below), we find that a *measure of the past*—cumulative history $H(t)$ —is a statistically reliable *predictor of the future*—the next dominance period T_i (Figures 3A and 3B). Specifically, the more a percept has dominated in the past, particularly recently (larger H value), the *shorter* the same percept (and the *longer* the other percept) dominates in the immediate future. These correlations were comparatively large and reached significance for 17 of 19 observers ($c_H = 0.24 \pm 0.1$ with $p < 0.001$ for KD displays and $c_H = 0.30 \pm 0.09$ with $p < 0.0001$ for BR displays). Thus, correlations with cumulative history were not only more consistently significant than but also twice as large as sequential correlations of dominance periods (Figure 4A). Parenthetically, similar results may be obtained with other kernels (e.g., half-Gaussian kernels that weighs the recent past more heavily than the distant past).

The highest correlation coefficients are obtained for each observer when the value of τ_H equals roughly half the mean dominance time T_{dom} (Figures 3C and 3D). Defining $\gamma_H \equiv \tau_H/T_{\text{dom}}$, the KD results showed maximal correlations for $\gamma_H = 0.54 \pm 0.21$, while the BR results exhibited peak correlations for $\gamma_H = 0.56 \pm 0.28$. The values obtained for τ_H are robust and not due to selection bias: when the data for each observer are divided in half and only one half is used to optimize τ_H , virtually identical correlation coefficients are obtained from the other half (not shown).

These observations are doubly significant. First, they show that perceptual dominance depends on prior perceptual history in a robust and consistently significant manner. Second, they reveal a characteristic time constant for this

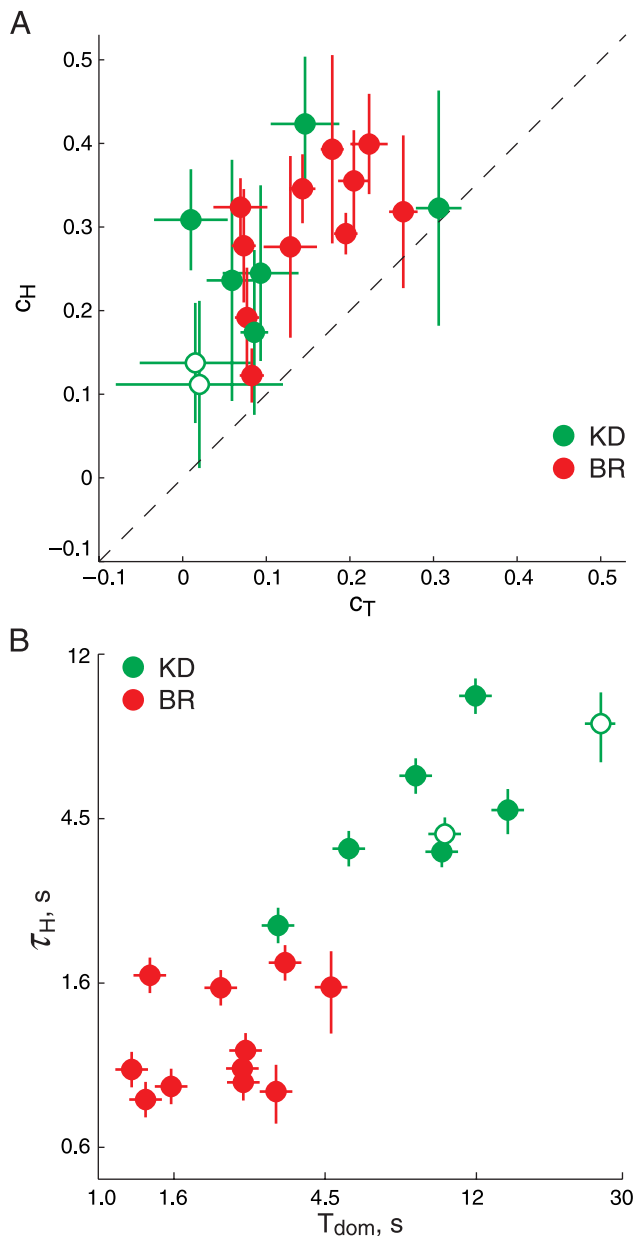


Figure 4. Scatter plot of observables. (A) Comparison between autocorrelation (c_T) and correlation with cumulative history (c_H). Open circles mark observers for whom c_H failed to reach significance. (B) Correlation between average dominance periods T_{dom} and decay constant τ_H , for 8 observers for KD and 11 observers for BR. Error bars represent standard deviation of bootstrapped means distribution for respective variable (see [Methods](#) section).

dependence, which is consistent with a gradual buildup of selective adaptation during perceptual dominance.

Interestingly, a buildup of selective adaptation is not the only factor to determine mean dominance times T_{dom} . As shown in [Figure 4B](#), the inferred time constant τ_H of neural adaptation correlates only loosely with the average dominance period T_{dom} . For both displays and all observers, the linear correlation coefficient was 0.825

($p < 0.001$). However, when each display is considered separately, the correlation drops to 0.64 ($p = 0.09$) for KD and to 0.36 ($p = 0.28$) for BR.

An analysis of transitional states—i.e., the “patchy” appearances of the BR display—suggests that, in the absence of any adaptive bias, perceptual reversals are driven by stochastic factors. Observers typically reported a “patchy” appearance during the transition from one uniform appearance to another (*forward transition*). Occasionally, however, a “patchy” period merely interrupted a uniform appearance, which afterward resumed (*return transition*; Brascamp et al., 2006; Hollins, 1980). Both *forward* and *return* transitions were profoundly affected by the balance of cumulative histories ([Figure 5](#)): “Patchy” periods lasted longer, and the *return* probability was far higher, when cumulative histories were approximately balanced and $\Delta H \approx 0$. In some observers, transitional states (which are often ignored in the calculation of

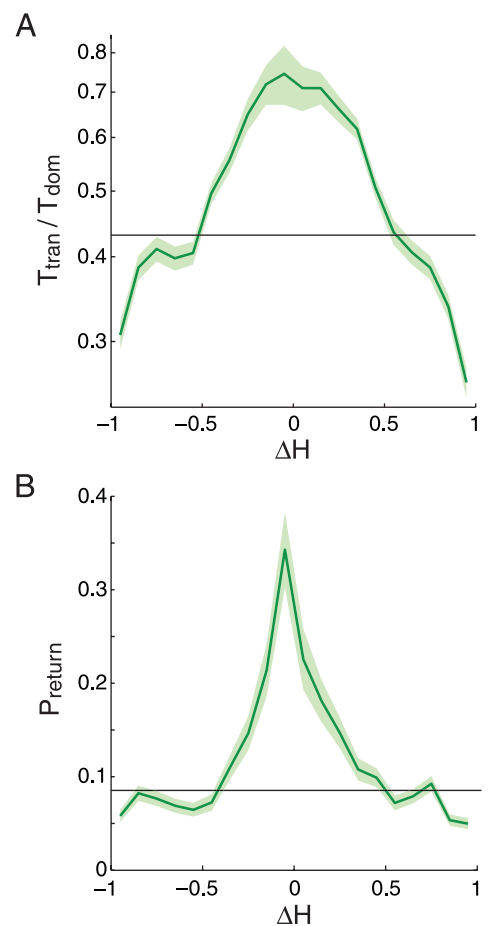


Figure 5. Transition periods depend on dominance history. (A) Transition duration (mean \pm standard error), in units of T_{dom} , as a function of history difference $\Delta H \equiv H_{red} - H_{green}$. For $\Delta H \approx 0$, transition durations increased 73% above their average value (black line). (B) Probability of return transitions (red→red or green→green) as a function of history difference ΔH . For $\Delta H \approx 0$, return probability rose fourfold above its average value (black line).

sequential correlations) even predict something about the subsequent dominance period. This is evident from the fact that some c_H values are larger than zero for very small values of τ_H (Figures 3C and 3D). Note that, for $\tau_H = 0$, the value of “cumulative history” corresponds directly to the identity of the preceding state ($H = 0, 0.5, \text{ or } 1$).

The total entropy of reversal timing can be computed from the distribution of dominance periods (see Methods section). From the joint distribution of future dominance periods and past cumulative history, one may further determine which fraction of the total entropy is shared between these two measures (mutual information). Using this approach, one finds that cumulative history accounts (on average) for approximately 9% of the entropy of reversal timing. Essentially, the same conclusion is reached when one compares the total variance of dominance periods with the variance that is explained by cumulative history (coefficient of determination). The fraction of explained variance is (on average) approximately 8.5%.

Discussion

We have introduced a novel statistical measure—*cumulative history*—to analyze serial reversals in the appearance of multistable displays. The results obtained with this measure go beyond earlier findings in several ways. First, they reveal a consistently robust and statistically significant correlation between past perceptual history and future dominance duration, which does not become evident with conventional measures such as sequential correlations of dominance durations (Borsellino et al., 1972; Fox & Herrmann, 1967; Lehky, 1995; van Ee, 2009; Walker, 1975). Second, they demonstrate that neural adaptation of the dominant percept raises reversal probability even when an ambiguous display is viewed continuously. All previous evidence on this point involved prolonged adaptation to non-ambiguous displays (Blake et al., 1990; Kang & Blake, 2010; Nawrot & Blake, 1989; Petersik, 2002; Wolfe, 1984). Third, they reveal the characteristic time constant of neural adaptation. Taken together, this constitutes the most compelling evidence so far that neural adaptation contributes to multistable dynamics.

Analyzing reversal sequences of kinetic depth and binocular rivalry displays, we found dominance periods to be correlated (on average) twice as well with *cumulative history* than with the immediately preceding dominance periods (Figure 4A). Moreover, correlations with *cumulative history* were significant in 17 of 19 observers, whereas correlations with earlier dominance periods were significant in only 5 of 19 observers. *Cumulative history* is a more informative measure because it integrates over several preceding dominance periods, taking into account both how long and how recently a particular percept has

dominated in the past. Due to its short time constant (see below), *cumulative history* assumes intermediate values only after one or more short dominance periods. In these (comparatively rare) situations, *cumulative history* is expected to be particularly predictive.

Even in terms of *cumulative history*, the effect of neural adaptation is comparatively weak and linear correlation coefficients do not much exceed 0.4. To properly gauge the influence of neural adaptation, it is helpful to compute its effect on reversal timing: cumulative history accounts for (on average) approximately 9% of the entropy and approximately 8.5% of the variance of reversal timing. These values should be considered a lower bound, because *cumulative history* is merely an estimate (and not an equivalent) of the true state of neural adaptation.

The fact that the influence of neural adaptation is so slight explains, of course, why it has proven so difficult to demonstrate this influence during the normal course of multistable perception. Accordingly, the timing or reversals must be dominated by factors other than neural adaptation. These “other factors” certainly include spontaneous fluctuations of neural activity (see below) and perhaps also volitional processes such as eye movements, eye blinks, or attention shifts (Leopold et al., 2002; Mitchell et al., 2004; van Dam & van Ee, 2006, but see Pastukhov & Braun, 2007).

Given an observed reversal sequence, one can typically determine the characteristic time constant for *cumulative history*. To this end, one compares the observed sequence with several hypothetical *cumulative history* time series, each computed with a different time constant. If at least some of these time series correlate significantly with the observed sequence, then the best-correlated time series provides a characteristic time constant for the observed sequence. Typically, the resulting time constants are comparable to the average dominance time, with a linear correlation coefficient of 0.825 (see Figure 4B), suggesting that *cumulative history* does indeed capture the time evolution of neural adaptation. Note, however, that most computational models of multistable perception (Laing & Chow, 2002; Lankheet, 2006; Moreno-Bote, Rinzel, & Rubin, 2007; Noest, van Ee, Nijs, & van Wezel, 2007; Shpiro, Moreno-Bote, Rubin, & Rinzel, 2009; Wilson, 2003) predict a strictly monotonic relation between average dominance times and the time constant of neural adaptation (sampling error apart). Our results are not consistent with such a strict correlation, even allowing for sampling error. Apparently, factors other than the time constant of *cumulative history* introduce additional variance in the mean dominance times. While there are many conceivable reasons for this partial dissociation, one intriguing possibility is that the collective dynamics of neural representations is partially uncoupled from the time constants of individual neural components (Braun & Mattia, 2010; Gigante, Mattia, Braun, & Del Giudice, 2009). Further work is needed to understand the full implications of this observation.

Our observations about transitional states suggest that the time course of neural adaptation is captured well by *cumulative history*. It has long been understood that the transition between two distinct appearances is informative about the driving forces of multistable dynamics (Brascamp et al., 2006; Hollins, 1980). In our binocular rivalry display, observers frequently reported transitional states in which both gratings were visible (“patchy” or “fused” appearances). In the kinetic depth display, transitional states were too rare to be analyzed. To ascertain the influence of neural adaptation on transitional states, we compared both the duration and the outcome of such transitional states with the *cumulative history* measure (Figure 5). We observed approximately 50% longer transition phases and approximately 200% more “return transitions” (i.e., transitions leading back to the preceding percept) when the difference between the two *cumulative histories* was close to zero, compared to the overall average values. The implication is, of course, that at other times—when neural adaptation of one percept exceeds that of the other—transitional states quickly make way for the less adapted percept. Thus, adaptive state, as captured by *cumulative history*, clearly plays a causal role in perceptual reversals.

Computational models of multistable phenomena propose that perceptual reversals reflect sudden shifts of neural activity that arise spontaneously within attractor neural networks (Braun & Mattia, 2010; Laing & Chow, 2002; Lankheet, 2006; Moreno-Bote et al., 2007; Noest et al., 2007; Shpiro et al., 2009; Wilson, 2003; Wilson, 2007). Presumably, a multistable display stimulates recurrent neural networks with several distinct steady states of neural activity (“attractor states”). If the stability of these steady states were not absolute but were continually undermined by neural adaptation and by neural noise, the result would be a continual sequence of sporadic reversals, in which one temporarily stable attractor state would suddenly make way for another such state. The degree to which such reversals would be driven by neural adaptation (“limit cycle dynamics”), by neural noise (“bistable dynamics”), or indeed by volitional processes remains unclear, although a number of recent studies have emphasized the importance of spontaneous activity fluctuations (neural noise; Kim et al., 2006; Lankheet, 2006).

Intuitively, attractor neural network models can be understood in terms of a double-well potential metaphor (Brascamp et al., 2006; Kim et al., 2006). Network activity is represented by a ball rolling on an energy landscape that is not static but continuously deformed by adaptation (Figure 6). Specifically, the floor of an occupied well is raised progressively by neural adaptation of the currently dominant percept. Simultaneously, as the other percept recovers from adaptation, the unoccupied well gradually becomes deeper. In addition to these deterministic effects, spontaneous activity fluctuations superimpose a diffusion-like dynamics and ensure that the energy landscape is widely explored.

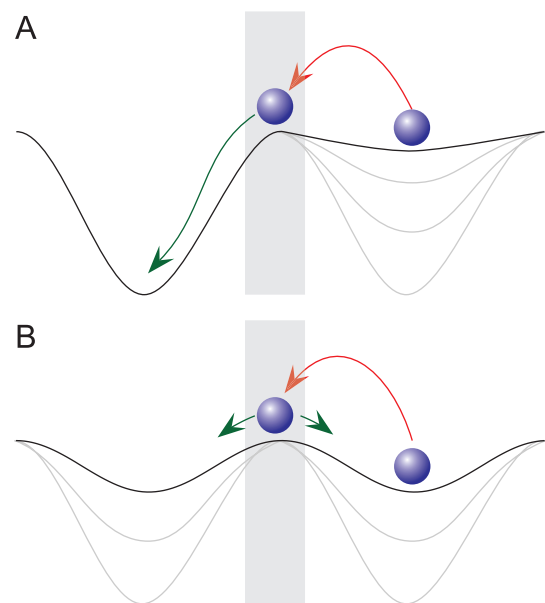


Figure 6. Double-well potential (schematic). (A) When one state fully adapted (right, high floor) and the other fully recovered (left, low floor), a transition initiated by a spontaneous fluctuation (red arrow) will terminate rapidly and deterministically (green arrow). (B) When both states are comparably adapted, a transitional state (red arrow) will terminate more slowly and more randomly (green arrows).

The double-well metaphor also accounts for our observations with regard to transitional states (Brascamp et al., 2006). Assume that perceptual reversals are initiated by spontaneous activity fluctuations of sufficient amplitude to overcome the energy barrier that separates the two wells. When one percept is highly adapted, the energy landscape will be asymmetric, with the suppressed percept being energetically favored over the dominant percept (Figure 6A). In this case, a transition will be rapid and its outcome will be deterministic. In contrast, when neural adaptation of the two competing percepts is balanced, the energy landscape will be symmetric and will consist of two comparably shallow wells (Figure 6B). The deterministic effects being weak, the diffusion-like nature of the dynamics will become evident: Transitions will be slow and their outcome will be random.

As reported in preliminary form (Rodríguez et al., 2010), our results are in detailed agreement with double-well potential models. If parameter values are chosen judiciously, the model of Laing and Chow (2002), for example, closely replicates the observed dominance times, their variability, and their (weak) dependence on prior dominance history. These results, which will be presented fully elsewhere, contradict a recent claim (van Ee, 2009) that only “slow” fluctuations in adaptive state can account for a weak dependence of dominance times on prior dominance history. In the hands of that author (van Ee,

2009), “fast” noise in neural activity (as postulated by double-well potential models) failed to produce a weak dependence on prior history. We question the generality of this negative finding and note that the combination of “slow” perceptual transitions and “fast” fluctuations of neural activity is readily accommodated by the theory of metastable states (Hänggi, Talkner, & Borkovec, 1990). A full discussion of this issue must await our forthcoming publication.

We conclude that adaptation of the dominant state plays an important causal role in dynamics of multistable displays. However, its effect is rather weak and limited to increasing the probability of reversals. The precise timing of perceptual reversals is determined largely by other factors, such as spontaneous activity fluctuations.

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