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Inertia and memory in ambiguous visual perception

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Abstract Perceptual multistability during ambiguous visual perception is an important clue to neural dynamics. We examined perceptual switching during ambiguous depth perception using a Necker cube stimulus, and also during binocular rivalry. Analysis of perceptual switching time series using variance–sample size analysis, spectral analysis and time series shuffling shows that switching times behave as a $1/f$ noise and possess very long range correlations. The long memory feature contrasts sharply with the traditional satiation models of multistability, where the memory is not incorporated, as well as with recently published models of multistability and neural processing, where memory is excluded. On the other hand, the long memory feature favors the concept of “dynamic core” or coalition of neurons, where neurons form transient coalitions. Perceptual switching then corresponds to replacement of one coalition of neurons by another. The inertia and memory measures the stability of a coalition: a strong

and stable coalition has to be won over by another similarly strong and stable coalition, resulting in long switching times. The complicated transient dynamics of competing coalitions of neurons may be addressable using a combination of functional imaging, measurement of frequency-tagged magnetoencephalography and frequency-tagged encephalography, simultaneous recordings of groups of neurons in many areas of the brain, and concepts from statistical mechanics and nonlinear dynamics theory.

Introduction

Few images are as fascinating as those whose appearance changes spontaneously (Attneave 1971). A classic example of perceptual ambiguity or multistability is the Necker cube shown in Fig. 1. When viewed steadily, the lower left side sometimes appears in the front of the cube, while other times it appears to be in back. Now imagine a different situation. If a horizontal grating were presented to the right eye while a vertical grating were presented to the left, the usual experience is of quasi-regular, but unpredictable, switches between the mutually exclusive perceptions: a second or two of seeing only horizontal lines and then a second or two of seeing only vertical lines, the phenomenon called binocular rivalry. Such multistable visual phenomena are of wide interest because they offer a starting point for investigating consciousness as well as visual information processing, perceptual organization, and the transition from sensation to perception (Blake and Logothetis 2002). An interesting variable that can be recorded during multistable visual perception is the switching time series. An important question to ask is: May the switching time series carry any interesting information about the dynamics of multistable perception?

Early studies on perceptual switching times focused on distributional properties of the time sequence and often assumed (but did not test rigorously) a stochastic

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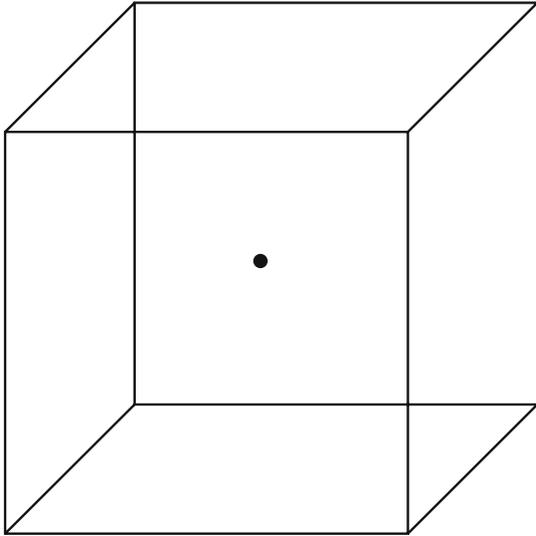


Fig. 1 Necker cube

system with independent events (Borsellino et al. 1972; Fox and Herrmann 1967; Walker 1975; Harris et al. 1988; De Marco et al. 1977). In order to infer valuable information about the dynamics of multistable perception, recently, the concept of low-dimensional deterministic chaos and fractal were applied to the analysis of switching time series, and found that the switching time series is not chaotic (Lehky 1995; Merk and Schnakenberg 2002), but is a type of $1/f$ -process (Aks and Sprott 2003), characterized by a power law decaying spectral density (Bassingthwaighe et al. 1994). Low-dimensional chaos is usually a consequence of nonlinear interactions among a few modes in a deterministic system. In principle, it is unlikely to be consistent with single unit neural recording and functional imaging studies, which implicate multiple cortical areas in visual multistability (Elbert et al. 1985; Inui et al. 2000; Kleinschmidt et al. 1998; Lumer et al. 1998; Tong et al. 1998; Sterzer et al. 2002; Steinbuechel 1998; Bisiach et al. 1999). This is because it is highly unlikely that the multiple cortical areas involved in visual multistability may be described by only a few variables.

What is the significance of $1/f$ -feature in the switching time series? $1/f$ processes often characterize spatiotemporal pattern formation in complex spatially extended systems (see Bak 1996; Press 1978; Wornell 1996; Gao et al. 2003 for classic examples; see van Leeuwen et al. 1997 on a coupled chaotic map model for perceptual switching), but is not a property of low-dimensional chaotic systems (Bak 1996). Such processes have been observed to appear in as diverse fields as traffic engineering (Leland et al. 1994), DNA sequences (Li and Kaneko 1992; Voss 1992; Peng et al. 1992), human cognition (Gilden et al. 1995), coordination (Chen et al. 1997), posture (Collins and De Luca 1994), and neural adaptation to natural images (Billock 2000; Billock et al. 2001). Of particular interest to our purpose is the study of Kelso (1995), which showed that $1/f$ distribution of

component frequencies at rest, extracted from large field magnetic activity in human cortex, can help assemble spatiotemporal patterns induced by presentation of meaningful tasks. Some $1/f$ processes may possess very long memories. In this paper, we address whether the $1/f$ feature of the switching times may indicate long memories in the data, and if yes, discuss how this memory may be related to the intriguing findings that activity in certain individual cortical cells during binocular rivalry is strongly correlated with the reported percept rather than being tied to the inducing stimulus (Logothetis and Schall 1989; Leopold and Logothetis 1996; Kreiman et al. 2002). To address these questions, we took a fresh look at our own previous data on the switching of Necker cube percepts (Merk and Schnakenberg 2002) and at new data on the switching of binocular rivalry.

Data

Two sets of switching time series were analyzed. The first one involved 11 subjects viewing a Necker cube (Fig. 1) displayed on a cathode-ray tube (CRT) with a viewing angle of 4° (small differences in orientation have little effect on distribution of switching times for this stimulus (Kelso et al. 1995)). Each subject fixated on the center of the display for 5 min at a time, indicating with a key press whenever the percept changed; ten such runs per subject were collected, with free rest in between to minimize fatigue and attention artifacts. Depending on individual switching speeds, each run produced 412–2,497 data points. Because fractal analysis requires long time series, we excluded data sets of less than $2^9 = 512$ points, retaining data from ten subjects. Figure 2a shows a representative experimental time series.

The second dataset was obtained in binocular rivalry experiments. Ten subjects participated in the binocular rivalry conditions using procedures described elsewhere (Pettigrew and Miller 1998). A 1° drifting horizontal grating was presented to the right eye while a 1° drifting vertical grating was presented to the left eye (or vice versa). The stimuli were 5 cycle per degree square-wave gratings drifting at 3 cycles per second presented in a 1° circular aperture, all centered within cross-hair and circular fixation guides. Each subject participated for 2 min at a time pressing mouse buttons to indicate their perceptual state. There were 14 such runs per subject with rests between runs at the subject's discretion. During a span of 28 min of data collection, the number of perceptual switches reported by the ten binocular rivalry subjects ranged from 652 to 936. Figure 2c shows a representative experimental time series for binocular rivalry. All the 20 datasets roughly follow gamma distributions (Zhou et al. 2004). A typical autocorrelation function for one of the switching time series is depicted in Fig. 3. While one might conclude such an autocorrelation function may indicate independence between the switching times, it is important to note that the autocorrelation is rarely identically zero, when the time lag is

Fig. 2 Individual time series for **a** a subject viewing the Necker cube, and **c** another subject viewing binocular rivalry. The shuffled versions of **a** and **c** are shown in **b** and **d**, respectively

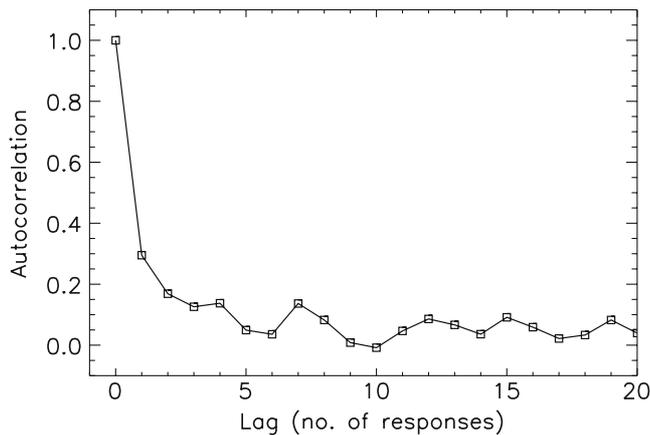
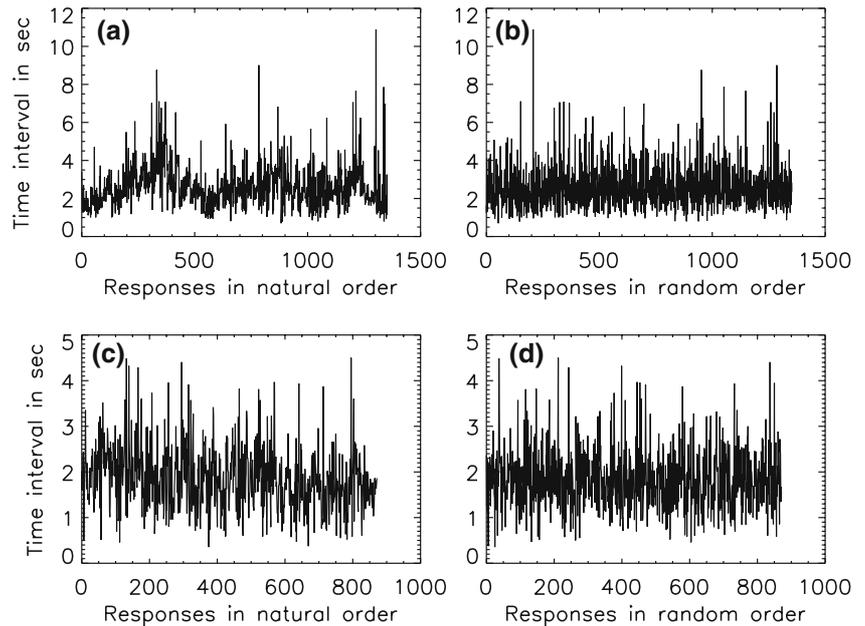


Fig. 3 A typical autocorrelation function

non-zero. One of our purposes here is to examine whether the variation of the autocorrelation with time lag, for a considerable range of the time lag, may contain interesting patterns, and if so, construe implications of such patterns. As is shown in the next section, the switching times indeed possess a pattern consistent with a long memory feature. Such long memory is sometimes called persistence.

Analysis

Persistence as a feature of the perceptual switching time series can be detected by analyzing non-overlapping running means. Specifically, let $x_t, t=1, \dots, n$, denote raw experimental data or switching times. We construct a new time series $X^{(m)} = \{X_t^{(m)}: t=1, 2, 3, \dots\}$, $m=1, 2, 3, \dots$, by taking non-overlapping running means of the switching times,

$$X_t^{(m)} = \frac{x_{tm-m+1} + \dots + x_{tm}}{m}, \quad t \geq 1.$$

For a random time series with fractal properties, the variance of the running means, $X_t^{(m)}$, declines in a power-law manner as the size of the sample, m , increases:

$$\text{var}(X^{(m)}) = \sigma^2 m^{2H-2}, \quad (1)$$

where σ^2 is the variance of the original time series x_t , and H is often called the Hurst parameter (Mandelbrot and Wallis 1969). When $H=0.5$, the process is called memoryless or short-range dependent, the most well-known example being white Gaussian noise and its integration being the standard Brownian motion (Bm) process. In such a process, $\text{var}(X^{(m)})$ drops to $\sigma^2/50$ when $m=50$. In nature and in man-made systems, often a process is characterized by $H \neq 0.5$ and then this reciprocal relationship between the variances and the sample size is lost. Prototypical models are fractional Gaussian noise (fGn), their integrals being the fractional Brownian motion (fBm) processes (Mandelbrot and Van Ness 1968). Processes such as fGn are often called increment processes, while those such as fBm are random walk processes. When $0 < H < 0.5$, we have negatively correlated increments in the random walk process; a jump up is more likely followed by a jump down and vice-versa. This leads to a process less nonstationary than Bm. Such a feature is called “anti-persistence” (Mandelbrot 1982). For $0.5 < H < 1$, we have positively correlated increments. This means that a jump tends to be followed by another jump in the same direction. This type of noise is more nonstationary than Bm, a feature called “persistence” (Mandelbrot 1982). Such processes have long memory properties. When $H=1$, the process has perfect correlation as in a linear ramp, where past states predict present ones.

To analyze our data for persistence (or anti-persistence) we calculated non-overlapping running means of the switching times, either in their natural order as in the time series of Fig. 2a, c, or else in a randomized order, the time series shuffled to obtain Fig. 2b, d, respectively. It is clear that the distributional properties of the original time series are preserved when they are shuffled. However, shuffling destroys any kind of correlation in the natural order of the original time series. These running means calculated with $m=50$ are plotted in Fig. 4a–d. Necker cube switching time means calculated from the natural time series (Fig. 4a) have a much larger variance than the same switching times shuffled before calculating their running means (Fig. 4b). The relationship between these variances is consistent with the H parameter of Eq. 1 having the value 0.84, the largest we found (see below). Binocular rivalry switching time means calculated from the natural time series (Fig. 4c) also have a larger variance than the same switching times shuffled before calculating their running means (Fig. 4d). In this case, the relationship between the variances is consistent with the Hurst parameter being 0.59, the smallest we found.

In order to estimate the Hurst parameter, we calculated $\text{var}(X^{(m)})$ for various m , and plotted $\text{var}(X^{(m)})$ versus m under log–log transformation as Fig. 5a. Note that in such a figure, a horizontal line corresponds to $H=1$, while a line with slope -1 corresponds to $H=0.5$. Figure 5a gives the results for the time series of Fig. 2a (upper solid line) and Fig. 2c (lower dashed line). We observe that those lines are fairly straight, especially when m is not too large. Due to the finite length of the time series, when m is large, then the estimation of $\text{var}(X^{(m)})$ becomes unreliable. This may be reflected in the steeper slope of $\text{var}(X^{(m)})$ with m as m approaches $n/2$. In fact, in order to minimize the unknown effect of

rests between successive runs in the perception experiments, we focused on such variance-sample size curves for m up to about 64, which is on the order of the average number of perceptual switches recorded in each run. The memory characterized this way can be considered a *lower bound* of the average memory for all runs—the memory computed from the concatenated switching times from all runs is an average memory from individual runs as well as between successive runs, the latter may actually be very close to zero. By focusing on such a range for m , simple linear regression from Fig. 5a finds slopes that, by substitution into Eq. 1, yield $H=0.84$ and 0.59 for the time series of Fig. 2a, c, respectively. Calculated Hurst parameters for all 20 subjects are shown in Table 1.

To evaluate the statistical significance of variance in the Hurst parameter, we estimated the sampling distributions for H . For each subject, up to 9,000 reshufflings of the time series were used to compute the likelihood of a given value of H arising from random orderings of the switching times. Figure 6 shows those empirical distributions for the same two subjects whose data appear in Figs. 2, 4, and 5 (solid line Necker cube, dashed line binocular rivalry). The means are close to 0.5 (the expected value for H for non-correlated random variables such as white Gaussian noise), with standard deviations ranging from 0.02 to 0.04 across the 20 subjects.

It can be proved (Leland et al. 1994) that when Eq. 1 holds, then the power spectral density (PSD) of the time series $x(t)$ follows $f^{-(2H-1)}$. The latter is indeed quite nearly so, as shown in Fig. 5b, where the upper and lower curves are for the PSDs of the time series of Fig. 2c, a respectively, and the two dashed lines are for $f^{-(2H-1)}$, with $H=0.59$ (upper) and 0.84 (lower). However, there are a few subtle points we should comment here: (1) Often, spectral analysis is applied to a time

Fig. 4 Non-overlapping moving averages of the time series of Fig. 2. The sample size for averaging is $m=50$

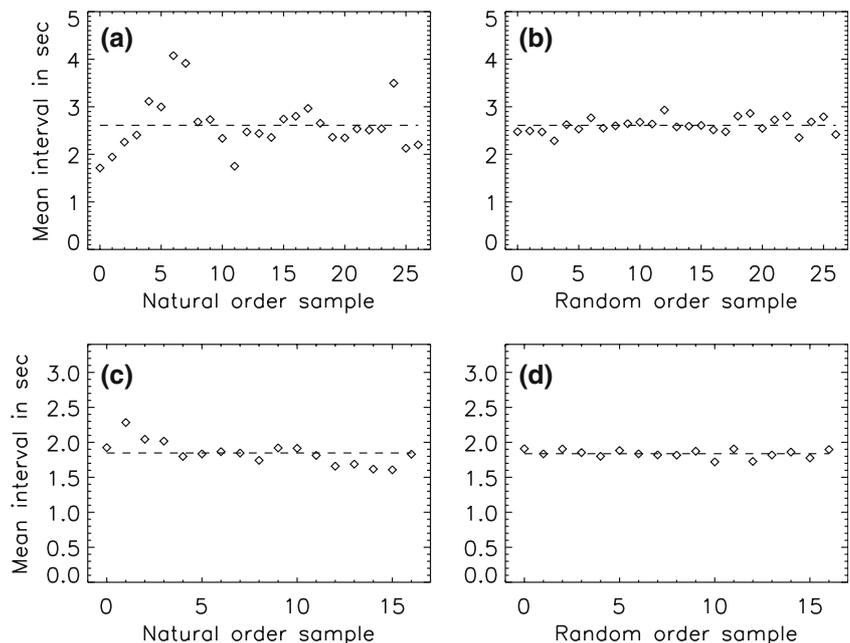
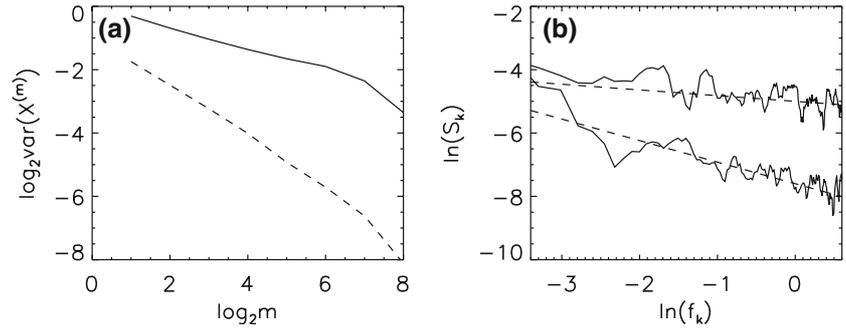


Fig. 5 a Variance–sample size plots for the time series of Fig. 2a (solid line) and Fig. 2c (dashed line). **b** Power spectral density for the time series of Fig. 2a (lower curve) and c (upper curve). The unit for the frequency is rad/s



series obtained by using a fixed sampling time interval. Switching time series are not generated in this way, however. Hence, one could ask, What is the meaning of the spectral density for the switching times? This paradox can be resolved by noticing that mathematically, Fourier transform is nothing but a way of expanding a complex function as a superposition of sine and cosine functions. What is shown in Fig. 5b is thus a representation of relations among the coefficients in the Fourier series expansion. At this point, it is appropriate to mention that typically equal time sampling is also required when autocorrelation is computed. In order to obtain such samples, we constructed an ON/OFF train from the switching time series, with ON and OFF representing the state that one of the two rivalry images was perceived. By sampling such ON/OFF train with a fixed time interval, we observed an autocorrelation function very similar to that depicted in Fig. 3. (2) When a time series is short, the PSDs may somewhat be variable, and the Hurst parameter estimated based on PSD might not be very reliable. It is interesting to note that Aks and Sprott (2003) reported an average $H=1$ for switching times based on the computation of PSD, and surmised that such a behavior might indicate some deterministic origin for multistable perception. In Gao et al. (2006),

we have shown that whenever H is either close to 0 or 1, there may be pitfalls in the analysis. However, we did not observe any H which is close to 1. We recommend that when the long memory feature of switching times is analyzed, PSD and other methods from random fractal theory should be used together to corroborate each other. We tried other methods such as detrended fluctuation analysis (Peng et al. 1994) and wavelet based approaches, and found consistent estimates for the Hurst parameter. (3) By Wiener–Kinchine theorem, the autocorrelation function and PSD form a Fourier transformation pair. Hence, the $1/f$ and long memory feature indeed characterize some pattern in the autocorrelation function. It should be emphasized that in principle, the autocorrelation function can also be used to estimate the Hurst parameter. In fact, theoretically, we have $r(k) \sim k^{2H-2}$, for large time lag k . However, such a relation is not very useful when a time series such as the switching times is not very long.

In some respects an H value in the neighborhood of 0.7 makes much more sense than a H value of 1. H values of around 0.7 are ubiquitous in nature (see Feder (1988) for a review and a table at p. 153 of computed exponents, which range from 0.63 to 0.79, with mean 0.74). They are also much closer to H values for music

Table 1 The Hurst parameter for natural time series from ten Necker cube and ten binocular rivalry subjects

Necker	Rivalry
0.63	0.59*
0.64	0.62
0.64	0.63
0.69	0.66
0.72	0.66
0.72	0.67
0.75	0.73
0.76	0.77
0.84	0.77
0.84	0.78

For 19 of these 20, the estimated likelihood was less than 0.001 (zero occurrences in 1,000 or more shuffles) that H in their shuffled time series was at least as large as H in their naturally ordered time series. For the 20th subject (indicated by *), whose H_{natural} was the smallest found, the estimated likelihood was 0.003 (30 such occurrences out of 9,000 shuffles)

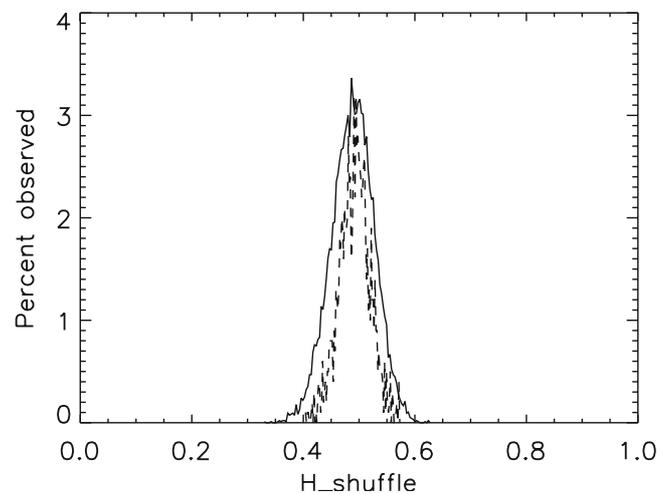


Fig. 6 The probability density function or sampling distribution for the Hurst parameter estimated from shuffled time series. The solid curve represents the Necker cube subject from Figs. 2, 4, and 5, while the dashed curve represents the binocular rivalry subject

and speech. If humans evolved and develop while immersed in a $1/f$ environment full of fractal time series, it makes sense that human perception would show compatible statistical behavior. On the level of aesthetics, Voss (1985) has suggested that this is why we like music: it is about halfway between randomness and predictability; orderly enough to not be dismissed as noise, but unpredictable enough to surprise us and keep our attention.

The scaling laws we find are truncated. This is to be expected for any experimental series, but it can also be a property of any physically instantiated fractal, especially in systems that suffer from physiological limitations (Bassingthwaite et al. 1994). The low-frequency range is truncated by the length of the series, but what truncates the high-frequency end of the power law? Subjects do not find that they cannot push the response key fast enough to follow perceptual switching, so the fundamental limitation on the high frequency range appears to be how fast the percept can change. In general, perceptual mechanisms involved in visual multistability are expected to follow the same limitations as ordinary visual perceptions; fundamental tasks in image processing like segmentation and grouping require about 50–200 ms (Marr 1980; von der Malsburg 1999), imposing a high-frequency limitation on the scaling law.

Summary and discussion

In summary, data shuffling, variance–sample size analysis, and spectral analysis established that Necker cube perceptual reversals and binocular rivalry switching times can each be characterized as a $1/f$ process possessing long-range temporal correlations (persistence). To facilitate the following discussion, we emphasize again that mathematically, such memory simply means that whenever a long switching time is observed, it is more likely for the next switching time to also be long, and vice versa.

A number of recent works seem to favor such a long-range memory feature: (1) Leopold et al. (2002) have reported that perceptual alternations can be slowed, and even brought to a standstill, if the visual stimulus is periodically removed from view. In such situations, switching times increased considerably, even to infinity. This can be considered infinite memory. Such phenomenon is more likely to occur in systems with memory than without memory. Similar arguments could be extended to studies which found that lesions of right precentral cortex seem to prolong Necker cube switching time (Steinbuechel 1998), lesions of right parietal cortex prolong binocular rivalry switching times (Pavlovskaya et al. 2001), as well as that binocular rivalry switching times are also unusually long in some psychiatric illnesses (schizophrenia and bipolar disorder) (Pettigrew and Miller 1998). (2) Leopold et al. (2003) have also shown that band-limited power (BLP) of local field potential (LFP) displayed fluctuations at many time scales.

Fluctuations at many time scales is a characteristic feature of fractal behavior. (3) Suzuki and Grabowecy (2002) have reported some evidence for perceptual “trapping” and adaptation, and argued that the hypothesis of “change-synchronization”, which refers to that eye dominance tended to be synchronized across the visual field, is not broad enough to interpret their evidence. “Trapping” and adaptation can be considered a type of memory, easier to occur in systems possessing memory.

In a recent interesting model, Murata et al. (2003) have suggested that in order for perceptual switching to occur, there may be several internal transitions involved. See the schematic of Fig. 7. Such a model can be analyzed from two different angles. One is to compute the probability for a switching as a multiplication of probabilities for each transition. This leads to log-normal distribution, which has been found to fit switching times excellently (Zhou et al. 2004). Alternatively, one may directly calculate the probability for the switching time as the sum of the times for each transition. If the time interval associated with each transition follows the same exponential distribution, then one readily obtains gamma distribution for switching times. Murata et al. (2003) have found that such a model with multiple internal transitions fits their switching time series well. By analyzing EEG signals measured during ambiguous perception, Nakatani and van Leeuwen (2005, 2006) have identified a few types of synchronizing and de-synchronizing events, consistent with such a model. In personal communications with the authors, Nakatani also points out that under the light of this model, the result of Leopold et al. (2002) can be readily understood: if stimulus is removed before a switching completes, the switching process has to start over again, therefore, enlongates the switching times considerably. Our finding of long memory in the switching times adds another attribute to such a model: the length of the switching times may indicate the energy barrier involved in the transitions. The higher the energy barrier, the more difficult the transtion is.

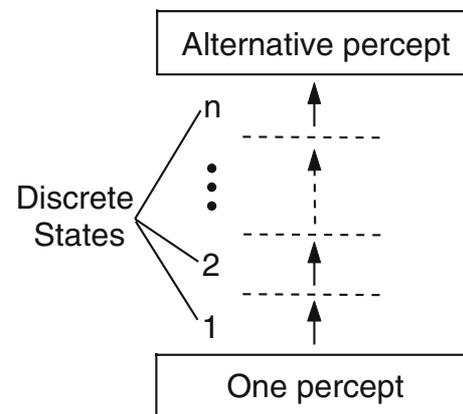


Fig. 7 A schematic showing stochastic transitions for perceptual switching

The long memory feature of the switching times has interesting implications. Traditional satiation models of multistability (Attneave 1971) do not incorporate memory per se. Even recently proposed theories (Laing and Chow 2002) and models (Leopold and Logothetis 1999) of multistability and neural processing and magnetoencephalography (MEG) studies of binocular rivalry (Tononi and Edelman 2000) have no place for the long-range correlations we find. The physiological correlates of these memory processes need to be explicitly addressed. One plausible framework is provided by the concepts of “dynamic core” (Edelman and Tononi 2000), or coalitions of neurons (Crick and Koch 2003). The latter scenario involves many types of excitatory and inhibitory interconnected neurons, which act by forming transient coalitions of neurons, the members of which support one another, directly or indirectly, by increasing the activity of their fellow members. This framework motivates us to speculate that during multistable visual perception, a sustained winning coalition of neurons may be responsible for one of the possible percepts formed. The winning coalition, however, may break down and subsequently be either replaced by a competing coalition or itself transformed into a different coalition. This corresponds to the switching of percepts. The memory may come from the inertia of the coalitions: a strong and stable coalition has to be won over by another similarly stable and strong coalition, resulting in long switching times. The stochasticity comes from the observation that each coalition is composed of a dynamic group of neurons. Being dynamic, the structure of the network of the coalitions of neurons, especially the connectivity of the network, must be highly transient. Such a coalition may involve a few or many groups of neurons in one or a few regions of the brain, while each group in a specific region is only a fraction of all neurons in that region.

If the above picture is plausible, one then can understand why “change-synchronization” (Suzuki and Grabowecy) is not broad enough. In fact, one has to conclude that variations of certain variables, such as neuronal firings, may not be uniquely mapped to a perceptual state. Such an inference seems to be supported by a number of studies: (1) It is well known that neuronal firing patterns are highly non-stationary. Hence, the correlation between the firing of a neuron and stimulus or a behavioral state has to vary with time too. (2) Gail et al. (2004) observe that multi-unit activity (MUA) does not have a one-on-one correlation with a perceptual state. This can be understood by noticing that MUA is an average over all the neuronal activities measured, while there may be only a few of the measured neurons that have contributed to a specific perceptual state; (3) Leopold et al. (2003) observe that the structure and coherence of BLP changes were highly similar under distinctly different behavioral states. Again, this may be because the BLP signals result from contributions from all the neurons in a specific brain area, while only a few of them are correlated with a specific behavioral state. (4) Such coalitions of neurons

may also be responsible for the many observations that many visually selective cortical cells in various parts of the visual pathways have activities that follow the multistable percepts, not the unchanging retinal input (Blake and Logothetis 2002; Logothetis and Schall 1989; Leopold and Logothetis 1996; Kreiman et al. 2002).

How might the above discussions be described quantitatively? For this purpose, let us employ concepts from nonlinear dynamics theory. Suppose each perception may be described by an attractor. Each attractor has its own basin of attraction. The basins of attractions live in an abstract mathematical space called phase (or state) space. Their shapes could be very complicated, even fractals, because of the dynamic nature of the coalition of neurons. Then perceptual switching is equivalent to jumping from one basin of attraction to another. Such jumping consumes energy. The length of the dwell time for each perception depends on where the system is in a basin of attraction. Then it is clear that inertia and memory is intimately tied with the size and shape of the basin of attraction. Different types of experimental designs and illnesses resulting in stabilizing percept or increasing switching times could be considered equivalent to effectively changing the relative sizes and shape of the basin of attractions.

While the above discussions have to be highly speculative at this stage, we hope that the complicated transient dynamics of competing coalitions of neurons may be addressable quantitatively using a combination of functional imaging, simultaneous recordings of groups of neurons in many regions in the brain, measurement of frequency-tagged EEG and MEG (Srinivasan 2004), statistical mechanics, such as symmetry breaking and phase transitions on various scales, and bifurcation and nonlinear dynamics theory, including the concept of “chaotic itinerancy” (Tsuda 2001; Kaneko and Tsuda 2003).

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