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Multistability in Perception Dynamics

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Synonyms

Ambiguous stimuli; Binocular/monocular rivalry; Multistable perception; Perceptual alternations; Perceptual bistability/tristability; Perceptual rivalry; Perceptual switching; Visual rivalry

Definition

Multistability in Perception Dynamics is the phenomenon of spontaneous switching in the subject's perception between different interpretations of an ambiguous sensory stimulus.

Detailed Description

When subjects are confronted with an ambiguous sensory stimulus for an extended time, instead of experiencing a fixed percept, they report spontaneous switching between the different interpretations, a phenomenon known as perceptual multistability.

In perceptual multistability, while the subject is aware of one percept, the others appear suppressed from consciousness. Moreover, the subject experiences constant switches from being aware to being unaware of a given percept. This phenomenon is thought to provide a powerful method to search for neural correlates of conscious awareness, since it allows to disentangle the neural response related to the physical properties of the stimulus, which is continuously present, from that related to the conscious percept (Rees et al. 2002; Sterzer et al. 2009).

Perceptual multistability, and especially perceptual bistability (two interpretations), has been extensively studied in the visual modality (see Leopold and Logothetis 1999; Blake and Logothetis 2002; Tong et al. 2006 for reviews). The paradigmatic example of perceptual multistability in the visual system is the so-called binocular rivalry, for which there exists a vast literature (see, for instance, Blake 1989; Tong and Engel 2001). In binocular rivalry two drastically different images (face and house, for instance; see Fig. 1a) are presented to the two eyes simultaneously, and perception alternates between these two images. Other examples of perceptual bistability in the visual system include the Necker cube (alternation of two depth organizations; Fig. 1b), Rubin's vase-face (alternation of two figure-ground organizations; Fig. 1c), bistable apparent motion (alternation of two arrangements of moving objects, Wallach 1935; Hupé and Rubin 2003; Rubin and Hupé 2004; see http://cerco.ups-tlse.fr/~hupe/plaid_demo/demo_plaids.html for a demonstration), etc.

Typically associated to the visual system, multistable perception has been reported in other sensory systems: auditory (Deutsch 1974; Pressnitzer and Hupé 2006; Bregman 1990), olfactory (Zhou and Chen 2009), and tactile (Carter et al. 2008). Recent studies suggest some common characteristics of perceptual multistability (Leopold and Logothetis 1999) across sensory modalities (Pressnitzer and Hupé 2006; see also Schwartz et al. 2012; Denham et al. 2012), namely:
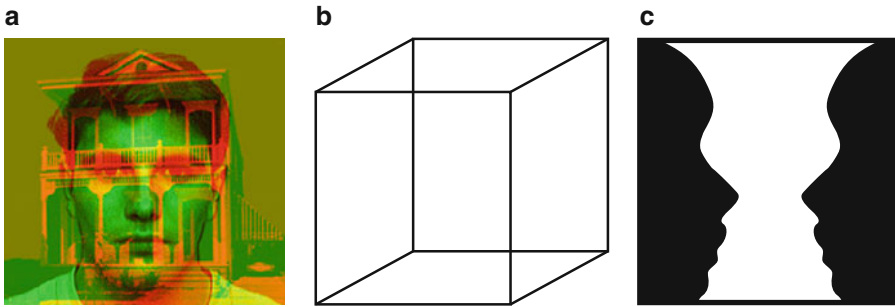
Multistability in Perception Dynamics, Fig. 1 Examples of visually ambiguous patterns (**a**) Face-house rival image created by Frank Tong and used in his fMRI study of binocular rivalry (reproduced from Tong et al. 1998 with permission from Elsevier); when viewed with *green-red* 3D glasses, perception alternates between a house and a face. (**b**) Necker cube; it can be perceived as a cube with the *lower-left* face or the *upper-right* face in front. (**c**) Rubin's face-vase; it can be perceived as a white vase or the silhouette of two black faces. Figures (**b**) and (**c**) from wikimedia commons

- Exclusivity. Conflicting visual representations are not simultaneously present.
- Inevitability. Given sufficient time, switching will ultimately occur. Some factors such as attention (van Ee et al. 2005; Meng and Tong 2004) and strong intrinsic or extrinsic biases towards one of the percepts (Lack 1978; Moreno-Bote et al. 2010) can slow switching down but do not eliminate it.
- Randomness. Durations of perceptual bouts follow log-normal (or gamma) distributions (Levelt 1968; Lehky 1995; Logothetis et al. 1996; Brascamp et al. 2005). Correlations between durations of successive perceptual bouts are absent or insignificant (Lehky 1995; Logothetis et al. 1996; Pastukhov and Braun 2011).

Since alternations occur not only when the inputs to the competing percepts are equal but also when they are largely unbalanced, one can study how changes in the stimulus' parameters affect perceptual dominance durations. For the domain of binocular rivalry, Levelt introduced a set of four "propositions" that summarize the effects of stimulus contrast of the monocular images on the switching dynamics (Levelt 1968). These properties, which are based on experimental observations, have been object of study in several works on perceptual bistability. Based on the existing literature, there is a general agreement on the reformulation of the second proposition. Thus, Levelt's updated set of binocular rivalry propositions state that:

(I) Increasing the stimulus strength in one eye will increase the predominance of the stimulus.
(II) Increasing the stimulus strength in one eye will affect the mean dominance duration of the eye with highest contrast (Brascamp et al. 2006; Boxtel et al. 2007; Klink et al. 2008; Moreno-Bote et al. 2010).
(III) Increasing the stimulus strength in one eye will increase the alternation rate.
(IV) Increasing the stimulus strength in both eyes will increase the alternation rate.

Although these propositions were originally described for the domain of binocular rivalry, dynamic properties for some stimulus manipulations in other bistable paradigms also satisfy them (Rubin and Hupé 2004; van Ee 2005; Klink et al. 2008; Moreno-Bote et al. 2010).

Neural Correlates of Perception

Experimental results in the visual system for subjects experiencing rivalry – imaging in humans and electrophysiology in awake, behaving monkeys – have revealed traces of neural activity that correlates with subject's perception at anatomically lower areas of visual processing (Tong and Engel 2001; Polonsky et al. 2000; Parkkonen et al. 2008), higher areas of visual processing (Leopold and Logothetis 1996; Tong et al. 1998; Leopold and Logothetis 1999;

Sheinberg and Logothetis 1997), as well as nonvisual parietal and frontal areas (Sterzer and Kleinschmidt 2007). Moreover, monkey electrophysiology (Leopold and Logothetis 1996) revealed that the proportion of neurons firing in time with perception increases along the visual pathway. Thus, while evidence of alternations is seen in different brain areas, the origin, which may involve interacting multiple areas, is still unknown.

Perceptual Multistability in Different Sensory Modalities: Auditory Streaming

Perceptual multistability has been extensively studied in the visual system. However, multistable perception has been reported in other sensory systems, in particular in the auditory system (see Schwartz et al. 2012 for a short review). Examples of multistability in the auditory system are found in binaural rivalry (Deutsch 1974), in the verbal transformation effect observed during word repetition (Warren and Gregory 1958; Warren 1961) and, especially, in the *auditory streaming* paradigm (Pressnitzer and Hupé 2006; Schnupp et al. 2010).

For the auditory streaming paradigm, the stimulus consists of a high-frequency tone A and a low-frequency tone B that are played alternately (AB-AB pattern) or in triplets (ABA-ABA pattern). For a slow presentation rate, the melody is perceived as a single stream that resembles a galloping (for the triplet pattern). However, if the presentation rate is fast enough and the frequency separation between the two tones is large enough, the melody is perceived as two separate streams (A-A-A-A and B-B-B-B). For intermediate values, there is ambiguity between coherence (a single stream) and segregation (two streams). These perceptual states were first reported by van Noorden in the so-called van Noorden diagram (van Noorden 1975). See Fig. 2. Later, experiments with long presentations reported alternations between these two states in the ambiguos region (Pressnitzer and Hupé 2006). Visit   http://auditoryneuroscience.com/topics/streaming-galloping-rhythm-paradigm   and
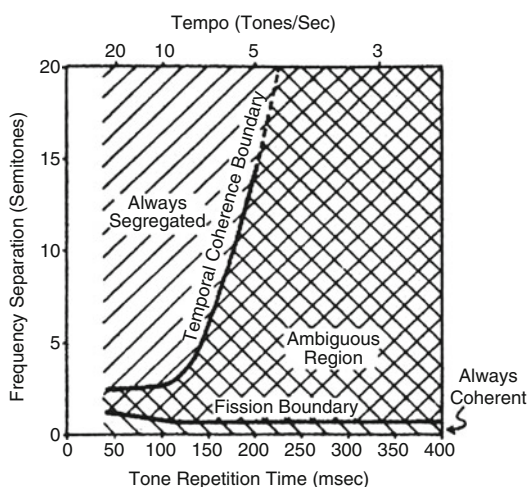
Multistability in Perception Dynamics, Fig. 2 Van Noorden diagram for the auditory streaming paradigm (Reproduced from McAdams and Bregman 1979 and adapted from Van Noorden (1975) with permission from the author)

http://auditoryneuroscience.com/topics/streaming-alternating-tones for a demonstration that illustrates auditory streaming.

As in visual multistability, perceptual correlations of neural activity have been observed in different brain areas. Recent studies indicate that perceptual auditory object formation, or "streaming," may be based on neural activity within the auditory cortex and beyond (Cusack 2005; Micheyl et al. 2005), as well as in early stages of the auditory pathway, such as the cochlear nucleus (Pressnitzer et al. 2008).

Some models have been developed for the auditory streaming paradigm (Almonte et al. 2005; Wang and Chang 2008; Mill et al. 2013). However, most of them try to account for the van Noorden diagram (see Fig. 2), rather than the dynamics of perceptual switches reported for parameters in the ambiguous region of the diagram (Pressnitzer and Hupé 2006).

Computational Models for Perceptual Switches

Current models of perceptual multistability are mainly phenomenological and try to explain the
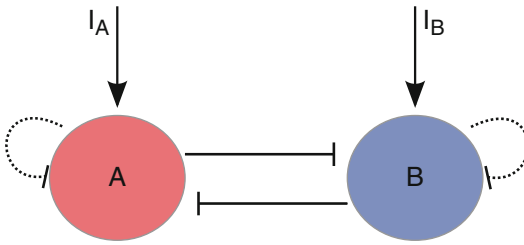
Multistability in Perception Dynamics, Fig. 3 Schematic representation of the network architecture consisting of two mutually inhibitory populations that code for the two competing percepts. In addition to the mutual inhibitory connections (represented by *solid lines*), neural populations receive excitatory synaptic input of strength I_i associated to the external stimuli and undergo self-adaptation (indicated by the *dashed* connections)

dynamics of perceptual switching with simple computational mechanisms. They mainly focus on visual bistable stimuli (just two competing interpretations) and especially on binocular rivalry. Among representative firing rate models, we find Lehky (1988); Mueller (1990); Wilson (2003); Laing and Chow (2002); Moreno-Bote, Rinzel, and Rubin (2007); and Kilpatrick and Bressloff (2010). While details vary among models, the mechanism underlying the alternating rhythmic behavior is similar. It involves competition between two neural populations coding for the competing percepts via reciprocal inhibition (the neurons generating the dominant percept inhibit the neurons coding the suppressed percept) and slow negative feedback in the form of spike-frequency adaptation and/or synaptic depression (over time the system fatigues allowing the suppressed percept to become dominant). See Fig. 3. Noise is added to the system to account for the irregular oscillations and, in some cases, to drive the switches, causing adaptation to play a secondary role (Kim et al. 2006; Brascamp et al. 2006; Moreno-Bote et al. 2007). These models do not usually specify the site at which these competing neural populations are located.

This framework (competition with mutual inhibition and adaptation) is, in principle, that of the half-center oscillator in models for central pattern generators, networks that drive opposing muscles for locomotion, respiration, swallowing, etc. (Hooper 2001; Brown 1914).

Mathematical Formulation

The firing rate models developed for perceptual multistability try to capture the qualitative aspects of the behavioral data with idealized models that avoid the overhead of detailed cell-based models. They assume that the relevant information is captured by the firing rate of each neural population. The mathematical formulation for the firing rate or activation dynamics r_i of the i-population (responsive to percept i) can be described by

$$\tau \frac{dr_i}{dt} = -r_i + f_i\left(\sum_j w_{ij} s_j r_j - \gamma a_i + I_i + n_i\right)$$
$$\tau_a \frac{da_i}{dt} = -a_i + r_i$$
$$\tau_s \frac{ds_i}{dt} = 1 - s_i + \phi s_i r_i$$

$$(1)$$

where I_i is the direct stimulus input, w_{ij} is the strength of the synaptic currents to population i generated by the rates r_j of the other competing populations j, a_i is the spike-frequency adaptation of population i (subtractive negative feedback), and s_j is the variable controlling synaptic depression of the synapses from population j (divisive negative feedback). The parameters γ and ϕ control the strength of spike-frequency adaptation and synaptic depression, respectively. The time scales for the slow self-adaptation τ_a (subtractive) and τ_s (divisive) are much larger than the time scale τ for the activation dynamics r_i of population i. Population's gain function f_i describes the steady-state output firing rate for constant input. It is usually assumed to be non-negative and monotonically increasing, typically taken to be a Heaviside, piecewise linear, or sigmoid function. Gaussian white noise or colored noise n_i is added to the differential equations for the neural responses r_i.

Parameters are tuned so that the models account for many features of the empirical data of the alternations (distributions of dominance durations, lack of correlations, etc.) and satisfy to some extent Levelt's propositions for stimulus parameter variations corresponding to binocular rivalry and other bistable phenomena.

What Drives the Switches? Adaptation Versus Noise; Oscillatory Versus *Winner-Take-All* Models

Schematically, the dynamics of switches for model Eq. 1 can be represented by a double-well-potential-type architecture coupled with noise (Brascamp et al. 2006; Kim et al. 2006; Moreno-Bote et al. 2007). The two perceptual states are represented by two wells and the current state is represented by the position of a ball within these wells (see Fig. 4). The ball initially settles into one of these wells. If adaptation is not present in the system, the depth of the wells will remain unchanged and the noise fluctuations will eventually kick the ball from the occupied well to the other one. See Fig. 4a. In Fig. 5a we show the time course of the activity of the two populations. But if adaptation is present, the wells will slowly change, depth decreasing for the well where the ball is located and then recovering when the ball is absent. If adaptation is strong enough, it will eventually destroy the energy minimum and form

a single well potential; the ball will roll towards the other well. See Fig. 4b. In Fig. 5b we show for the time course of the population activity and the adaptation. However, if adaptation is weak, it will only reduce the depth of the well but without destroying the local minimum. As in the adaptation-free case, the noise will be the ultimate responsible of kicking the ball to the other well. See Fig. 4c. In Fig. 5c we show the time course of the population activity and the adaptation.

Thus, one can distinguish between *oscillatory models* (slow adaptation causes alternations by itself) and *noise-driven attractor models* (noise drives switches in a winner-take-all framework). For noise-driven attractor models, the deterministic system (without noise) has two stable fixed points (attractors) (Figs. 4a and 5a). Such a system may incorporate adaptation, as long as it is weak enough so that it does not destroy the stable fixed points (Figs. 4c and 5c). For those models, if noise is removed, the system will remain indefinitely in one of the attractors. For oscillatory

Multistability in Perception Dynamics, Fig. 4 Double well potential landscape for three models of perceptual bistability: (*b*), (*a*) noise-driven model without adaptation, adaptation-driven model, and (*c*) noise-driven model with weak adaptation. The position of the ball represents the perceptual state at a given moment. Adaptation slowly modulates the potential landscape
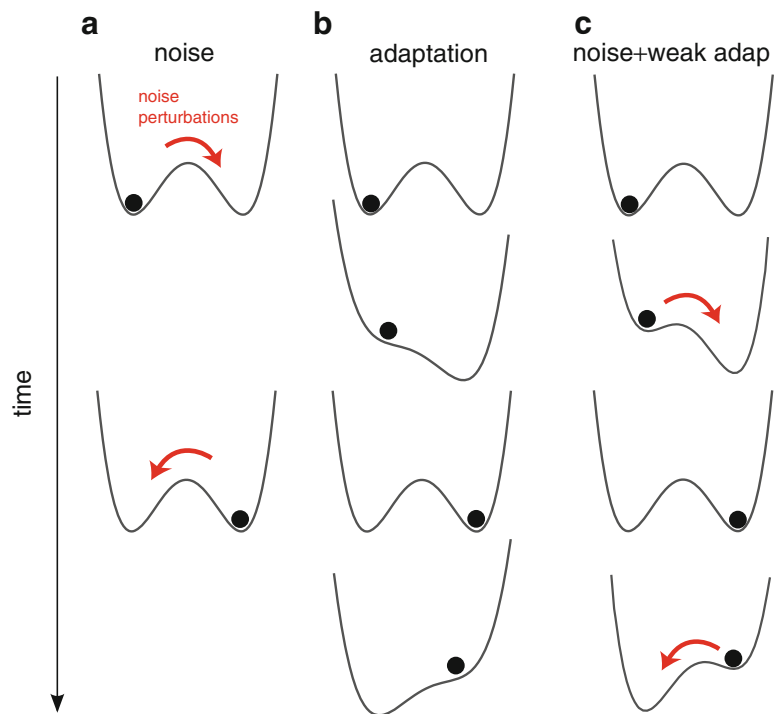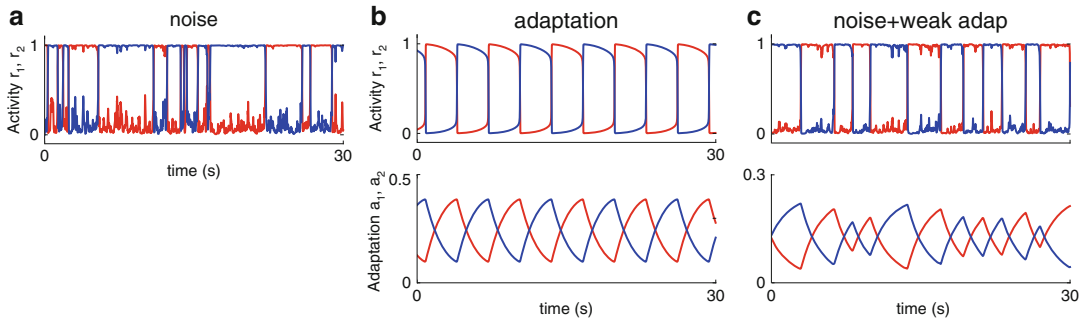
Multistability in Perception Dynamics, Fig. 5 Time courses of activity and adaptation for the two populations coding for two different percepts for (*b*), (*a*) noise-driven model without adaptation, adaptation-driven model (*c*), and noise-driven model with weak adaptation

models the deterministic system does not have stable fixed points but a stable limit cycle, with most of the time spent in the wells (Figs. 4b and 5b). For such a system, noise can be incorporated (e.g., to account for the variability in the dominance durations) as long as it does not destroy the limit cycle. To assess the role of noise and adaptation, the models try to conform to experimental data on dominance durations (averages, histograms' shape, correlations between successive durations, etc.) and Levelt's propositions. Several studies suggest that models should operate in the noise-driven regime but not far from the boundary of being adaptation driven (Moreno-Bote et al. 2007; Shpiro et al. 2009; Pastukhov et al. 2013; Huguet et al. 2014).

Indeed, for white noise-driven attractor models, the residence times in each state will be exponentially distributed; switching is a Poisson process, described by Kramer's rate theory (Kramers 1940). For adaptation-driven oscillator models, the residence times are regular, and adding noise will only perturb them around the mean; the distributions will look symmetrical around the mean. If adaptation is weakened, effectively giving more strength to noise, the histogram gradually evolves into a skewed one (log-normal or gamma as observed in the experiments). Thus, noise-driven models provide more variability and weak adaptation precludes short

perceptual durations. In the double-well framework, the ball must wait for adaptation to adequately reduce the barrier before leaving the well, thus preventing the ball from leaving immediately after settling into the well.

Noise and adaptation should be set within some appropriate range so that correlations between successive perceptual durations are weak or absent, consistent with the experimental data. Indeed, if adaptation is too strong, during a long phase of dominance, the active population recruits a lot of adaptation, and when this population becomes suppressed, a long phase of recovery will be necessary before the next switch can occur. In the double-well case, if the ball jumps from one well after a long residence time, it falls into the other, now very deep, well; the barrier between wells is very high and the ball must wait a long time before it can switch back. These relations between successive durations lead to strong positive correlations.

Finally, for mutual inhibition models (irrespective of being noise or adaptation driven), one can distinguish two mechanisms for which transitions may take place: escape and release. For the release mechanism, the dominant population weakens (due to the slow self-adaptation) allowing the suppressed one to take over. However, for the escape mechanism, the suppressed population takes over after recovering from self-adaptation, suppressing the active population.

In Shpiro, Curtu, Rinzel, and Rubin (2007), the authors identified these two mechanisms in different parameter regions for the models in Laing and Chow (2002) and Wilson (2003) as well as other models based on mutual inhibition. They found that these models only satisfy Levelt's IV proposition when set in an escape mechanism. In Seely and Chow (2011), various biophysically plausible modifications to mutual inhibition models are proposed to resolve this issue.

Other Models of Perceptual Bistability

Centralized Mechanism of Perceptual Decision

Pettigrew and colleagues (Carter and Pettigrew 2003; Sheppard and Pettigrew 2006; Miller et al. 2000) conjectured the existence of a single oscillator external to the level of sensory representation that drives the switches, based on their results showing strong correlations of switch rates across subjects for different visual bistable stimuli. They proposed that oscillatory activity in the brainstem/subcortical area may generate rhythmic fluctuations in activity across the two cortical hemispheres. This would lead one to expect similar dynamics for bistable perception in different modalities. However, some studies reported absence of correlation across modalities for subject-specific biases (Pressnitzer and Hupé 2006; Carter et al. 2008).

Winnerless Competition Models

Winnerless competition models propose a mechanism for perceptual dynamics based on deterministic trajectories moving along heteroclinic orbits that connect saddle points in the phase space (Rabinovich et al. 2001). The saddles correspond to the activity of specific neurons or group of neurons and the heteroclinic orbits connecting the saddles correspond to the switches between different states. Winnerless competition models are not multistable; states are represented by transient trajectories close to the saddles rather than attractors of the noiseless system. The models can account for properties such as distribution of dominance times and Levelt's propositions (Ashwin and Lavric 2010).

Models of Percept Formation

Most models focus on the dynamics of perceptual alternations assuming that the percepts and their neuronal representations are given. Other models have been developed to account for the form of the generated percepts. Diekman, Golubitsky, and Wang (2013) presented an algorithmic-like model based on Wilson's networks to account for interocular grouping percepts in binocular rivalry (Kovacs et al 1996; Suzuki and Grabowecky 2002). These percepts are new images generated from features extracted from the images presented to the left and right eyes. The model considers neural populations that code for a particular image feature (such as color, orientation, motion direction, position, etc.). Neural populations that code for features of the presented images have excitatory connections. The model then looks for bifurcations from a fused state to an oscillatory state, in which several competing percepts alternate. They can also predict the form of the conflicting percepts, which in the case of interocular grouping contains features from both presented images.

In the auditory domain, Mill et al. (2013) proposed a model that looks for predictable patterns from the ongoing sequence of tones. These patterns are then strengthened or weakened based on their predictive success. The ones that are strengthened and thus maintained compete with other representations, creating perceptual multistability.

Perceptual Multistability with More Than Two Interpretations

Results on ambiguous sensory stimuli with more than two interpretations are still scarce in the literature. However, more than two percepts allow us to go beyond the temporal dynamics and explore transitions to different states. Recent results suggest that switches are not totally random but there is some dependence on perceptual history and/or trapping (Suzuki and Grabowecky 2002; Naber et al. 2010; Wallis and Ringelhan 2013; Huguet et al. 2014).

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Further Reading

Binocular rivalry: http://www.scholarpedia.org/article/Binocular_rivalry

Gestalt psychology: http://en.wikipedia.org/wiki/Gestalt_psychology

Multistable perception: http://en.wikipedia.org/wiki/Multistable_perception