

From one to many (and back again): an alternating renewal process describes the dynamics of bistable perceptual grouping

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Abstract

The buildup over time of split percepts for ambiguous stimuli, especially the buildup of stream segregation, has previously been accounted for by feedforward processing as a consequence of the accumulation of adaptation over time. However,

Author Summary

Introduction

For some stimuli in the visual and auditory modalities with ambiguous grouping cues, there is a tendency for the likelihood of perceptual "splitting" to increase with time. For instance, with ambiguous moving plaids constructed from moving square wave gratings at intermediate speed and angle, observers have consistently reported first experiencing motion coherence, even when steady-state perception is biased towards transparent motion of the individual gratings [1]. Analogously, for ambiguous tone sequences in which observers report alternations between hearing grouped triplet patterns and split streams [2] (see Figure 1), there can be an initial period of buildup over which the probability of stream segregation increases.

Buildup is thought to reflect the accumulation of evidence by the sensory system to support the representation of multiple objects in a complex scene [3], or alternatively the accumulation of multi-second habituation of the neurons processing sensory inputs [4], [5]. However, we show that this need not be the rule for the neural hardware underlying the subjectively sudden, random switches between perceptual states; instead, the gradual increase in probability of a split percept over time could reflect the dynamics of an entirely random underlying alternating renewal process with a given initial state.

The process of constructing empirical buildup curves involves the averaging over many trials of the timecourse of a random binary state variable (see Figure 2, blue lines). In our statistical model, the initial state (percept) is fixed, but the dwell time in this state is a random variable characterized by its probability density function. Subsequently the system switches randomly between two states, each of which has its own fixed duration distribution.

Results

Alternating renewal process

The long-term dynamics of perceptual bistability consist of alternations between mutually exclusive percepts. The duration histogram of each percept is well-fit by a gamma density [6]. We believe that the short-term buildup in probability of split percepts, observed when short trial perceptual timecourses are averaged, could reflect the dominance duration distributions observed over long trials. To examine this

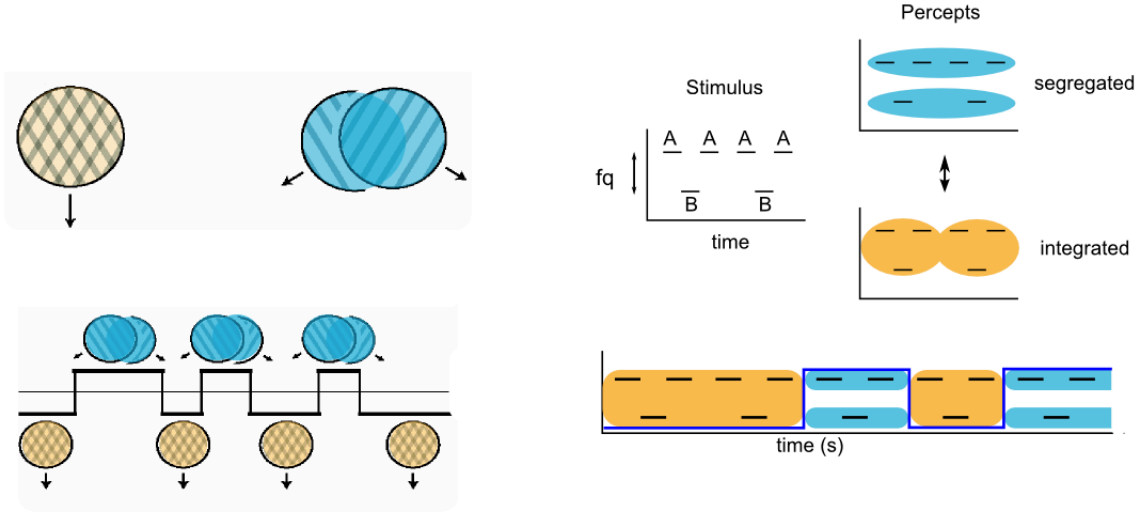


Figure 1: Examples of stimuli that can produce ambiguous grouping. Left, image adapted from Rubin and Hupe (2004). Moving gratings at certain angles can produce ambiguous motion. Observers report alternations between coherent and transparent motion of the component gratings. Right, van Noorden triplets with ambiguous stream segregation. Listeners report alternations between hearing integration and segregation of the component tone frequencies.

relationship we use the theoretical framework of an alternating renewal process. In this investigation we show that these distributions of percept durations, without any mechanism for accumulation, can account for the experimentally observed dynamics of buildup for a stimulus with ambiguous grouping, as follows:

1. the perceptual state alternates back and forth between grouped and split
2. the durations for these perceptual epochs are random, independent and stationary
3. the initial percept on a given trial is always the grouped percept

This theoretical framework ignores history dependence between perceptual epochs. We initially tested this theory in Monte Carlo simulations by simply constructing *in silico* perceptual timecourses according to the above assumptions (see Figure 2, (a)). For a given simulated trial timecourse, we draw alternating random samples from each of two distributions– one corresponding to the grouped and one to the split state durations. We begin with the distribution corresponding to the grouped state, and continue drawing samples until the sum of all the durations exceeds the length of a trial. These trial durations are converted into discretized timecourses by assigning a value of 0 to time intervals during which the state corresponds to a grouped percept, and assigning a value of 1 to the time intervals for which the percept state was split. In Monte Carlo, we produce an arbitrarily large number of such trial timecourses, then take the average at each time point.

We have also derived an analytical solution to this process. There are a number of advantages to characterizing the buildup function in this way. First, with an analytical solution relating the distributions of durations for grouped and split percepts to the buildup function, it is theoretically possible to interconvert between buildup functions and the statistics of the dominance durations for each percept. We have developed this solution into a statistical switching model to reconstruct the buildup function from four parameters- the parameters

for the gamma densities for grouped and split percepts. This theoretical solution coincides with the Monte Carlo results (see Figure 2, (b)). This is convenient, as the analytical solution is both computationally less expensive than iterative Monte Carlo simulation, and the solution is exact. Furthermore, in the alternating renewal process framework, there is no need to directly account for any mechanism of accumulation. Therefore, this formulation challenges the conventional understanding of buildup of sound source segregation as a gradual accumulative process.

Competition model simulations produce buildup as a consequence of alternations

Previous work (Wilson & Cowan, Laing & Chow, [6], [7]) has used population firing rate models with competition architecture to model perceptual bistability. In these pseudoneuronal mutual inhibition models, there are separate populations whose firing rates represent the perceptual strength of each interpretation of the stimulus. These models were originally developed to describe binocular rivalry, but have also been used to account for the psychophysical results of experiments with ambiguous grouping—namely, moving plaids with coherent/transparent motion (Shapiro, L&C) and triplets with streaming integration/segregation (Denham?).

In competition models, the relative firing rates of the two populations are taken to produce the simulated observer’s perceptual reports. The population with the higher firing rate corresponds to the dominant percept. Because the two populations mutually inhibit each other, in most cases only one population is active at any given time. In addition, each population undergoes adaptation in response to its own firing rate. The alternation of dominance epochs between the two populations can be driven by two mechanisms— if adaptation is strong enough, then the drive on the dominant population will decay over time, while the suppressed population recovers from any prior adaptation. This leads to periodic alternations between dominance states with oscillation dynamics. However, if adaptation is weak, the system will display attractor dynamics, in which alternations are driven by noise in the externally applied inputs.

The difference between oscillator and attractor dynamics in these competition models is most simply understood by observing how the system would behave without noise [6], [?]. For oscillation dynamics, slow adaptation would cause the dominant population to reduce its activity over time, reducing the inhibition on the suppressed population, allowing it to become active. In a noiseless system, stable fixed points in the system to appear and disappear over time, and alternations will occur deterministically with a constant period. Noise in such a system will affect the distribution of dominance durations for each state, but is not required for switching. Conversely, attractor dynamics occurs when a system has multiple stable states at the same time. In the absence of noise, the initial conditions determine which state becomes active, and the system behaves in a winner-take-all fashion. That is, the population that becomes dominant first is permanently active, and the other population is permanently suppressed. However, injecting noise into such a system can cause switches from one stable state into another. In this case, the switching between perceptual dominance states would be caused by the noise itself. The brain appears to be a very noisy system, with random fluctuations occurring at multiple scales such as vesicular release and spiking variability.

We wanted to use the competition model as a test-bed for the theory of the alternating renewal process. **We chose initial conditions that ensured that the grouped percept was always dominant at the beginning of the trial, as our hypothesis that alternations could produce buildup relies on this assumption.** We did this in the simplest manner possible (see Figure 3), by setting the initial condition on the population representing the grouped percept to half its maximum value. All other initial conditions were set to 0. From the population firing rates we computed dominance durations, which were converted to binary timecourses and averaged over trials to produce competition model buildup functions.

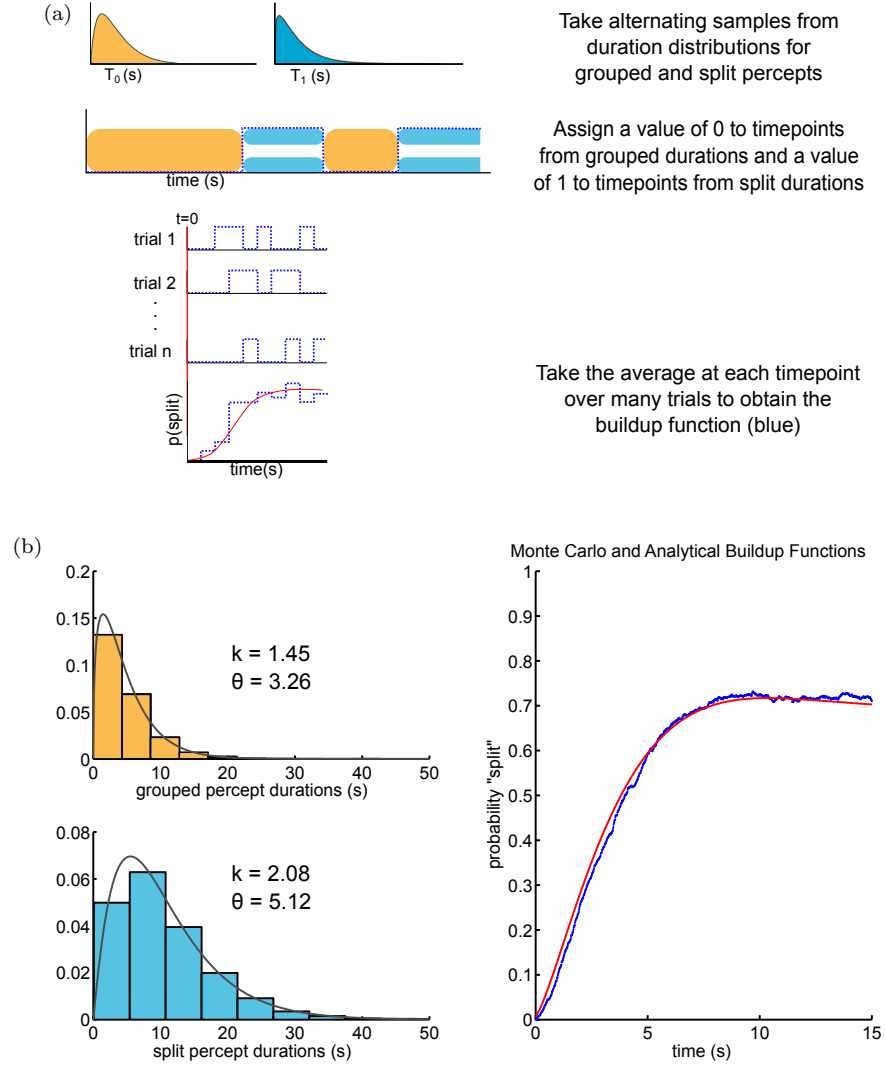


Figure 2: **(a)** Visualization of the alternating renewal process producing a buildup function. We used gamma probability density functions approximating duration distributions to construct Monte Carlo simulations. The analytical solution to the alternating renewal process model, shown as a red solid curve (bottom), allows us to predict buildup as a function of the distributions of dominance durations of each of the perceptual states. **(b)** Monte Carlo computed buildup function of 1000 trials (blue) approaches the theoretical solution (red). Gamma distribution parameters chosen from fits to a preliminary psychophysical dataset (not shown).

Using this method, we produced buildup functions for both oscillator and attractor competition models.

To test the application of the alternating renewal process model, we viewed dominance durations of each state from the short simulated trials as samples from underlying gamma distributions. Because our competition model simulations generated trials that were only 20 seconds long, a large proportion of these durations were truncated by the end of the trial. We estimated gamma parameters k and θ that maximized the likelihood of the complete as well as the right-censored dominance durations for each model "perceptual" state. Using only the four parameters so obtained, we were able to get very strong fits to the buildup function (R-squared > 90%).

Psychophysically observed buildup is inconsistent with alternations under oscillation dynamics

Previous work from our lab has shown that oscillation dynamics are inconsistent with a number of statistical features of the dominance durations reported in psychophysical experiments [6]. The mean and circular variance of dominance durations under this dynamical regime do not fall within the range of those observed for perceptual reports of ambiguous visual displays. Furthermore, when adaptation drives alternations in the dominance of population activity, we observe moderate and significant correlations between successive percepts. Data from the psychophysical literature suggests that the durations of subsequent percepts are only weakly correlated, if at all [?].

We wanted to examine buildup under each of these dynamical regimes in order to determine whether we could find correspondence between the buildup functions produced by competition models and those reported in the psychophysical literature. Previously reported psychophysical data suggest that buildup is largely a monotonic process. To our knowledge, no psychophysical experiments have shown a buildup timecourse with a damped oscillatory approach to steady state. Buildup functions produced under oscillation dynamics in our competition model (Figure 4), however, display damped oscillations reflecting the underlying periodicity of the mechanism of alternation.

Alternations with attractor dynamics, however, produce buildup functions that are mostly monotonic. By computing the buildup function produced under different dynamical regimes, we find converging evidence with previous studies that distinguish attractor dynamics from oscillation dynamics—when the competition model operates with oscillation dynamics, the buildup function is inconsistent with psychophysically observed buildup functions.

Discussion

Do percept-to-percept correlations matter for describing buildup in an alternating renewal process?

The previous competition model simulations provide a test-bed for our novel statistical model. When given dominance durations are not statistically independent, and there is history dependence between successive perceptual epochs, can the alternating renewal process theory still relate buildup to the underlying duration distributions? We measured the correlations in the data produced for noise-driven and adaptation-driven alternations. As previously reported, the adaptation-driven perceptual timecourses showed moderate correlations between the durations of successive percepts. Our statistical model, however, ignores this history dependence entirely, treating the distributions of percept durations as entirely independent.

Importantly, even for adaptation-driven switching, for which history dependence between successive durations is prominent (r value of 0.23), the buildup function predicted by the alternating renewal process without any consideration for correlations matched the competition model simulated buildup function with a coefficient of determination of 93%. We believe that the failure of history dependence to affect

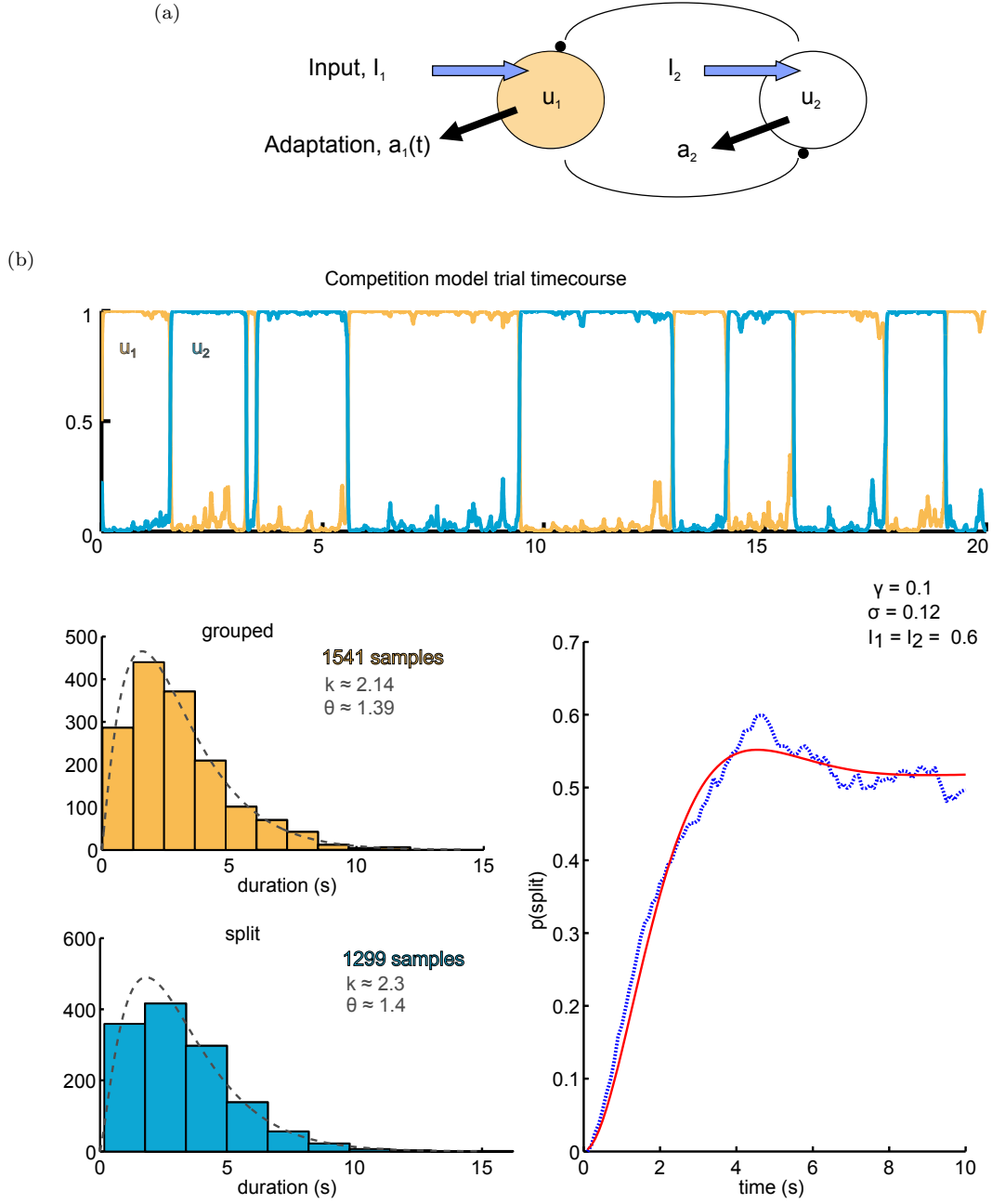


Figure 3: **(a)** Mutual inhibition population firing rate model producing buildup. Two neural populations u_1 and u_2 , each representing one possible interpretation of a stimulus, are driven by constant external input I , representing the external cues in favor of one or another percept. The populations mutually inhibit each other, so that only one can be dominant at a given time. In addition, they each undergo slow spike frequency adaptation. We choose initial conditions to ensure that the population representing the grouped percept, u_1 , is always dominant at the beginning of a given trial timecourse. **(b)** Competition model simulation results for parameters that produce attractor dynamics with noise-driven switching. Top, population activity timecourse for one 20-second trial. 500 trials were simulated to produce the buildup function, lower right (blue). Histograms of the dominance durations, with maximum likelihood estimated gamma density parameters, are shown in the lower left. These parameters allow us to compute analytically the resulting buildup function (red). The buildup function looks similar to those reported in the psychophysical literature, and the ARP prediction is good (R-Squared = 98%).

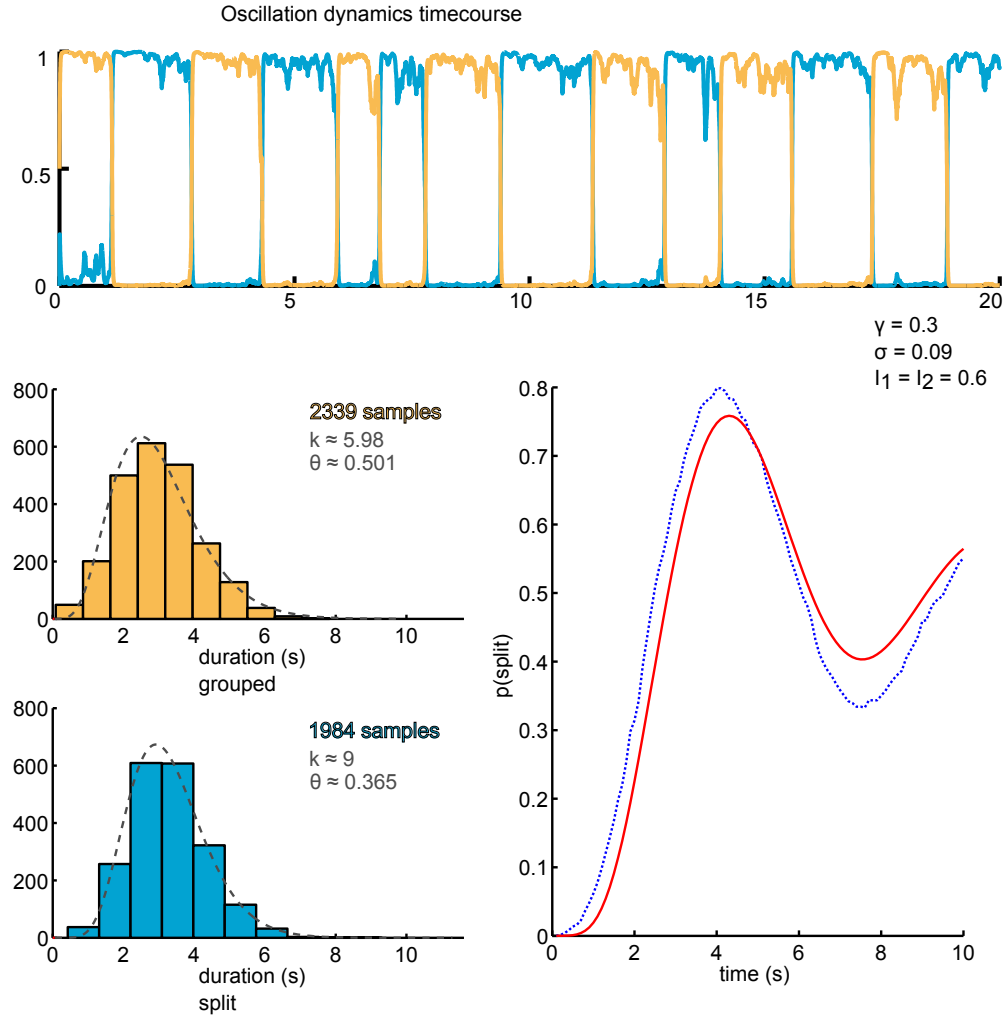


Figure 4: Competition model simulation of buildup under oscillation dynamics, for which switches between dominance states are driven by adaptation. Top, an example trial timecourse. The dominance durations are much more regularly timed, reflecting the clock-like periodicity of the underlying oscillator. These oscillations are dramatically present in the average. The prediction under the alternation hypothesis from the gamma parameters is still quite good (R-squared = 93%).

the dynamics of buildup results from the loss of information about individual trial timecourses caused by averaging. While the correlations between perceptual epochs may be important for understanding the timecourse of a particular trial, the correlations between specific perceptual epochs are "washed out" by taking the average of many timecourses. Therefore, the dynamics of buildup can be described purely by the underlying distributions of dominance durations.

Previous accounts of buildup [4] [5] have pointed to the accumulation of adaptation as a critical feature for the switch from a grouped to a split percept. Indeed, multi-second habituation in the auditory periphery [5] can predict the behavioral buildup of streaming. It may therefore be surprising that the alternating renewal process neglects to account for adaptation entirely. We believe that previous observations and our own can be reconciled, and may even be complementary. Previous work provides some account for how the switch from the grouped to the split percept might be accomplished as a result of an accumulation of adaptation. While we do not explicitly invoke an accumulative process to describe this switch, the use of a gamma density to describe the distribution of dominance durations for the grouped percept implies history dependence. This is because the hazard function for a gamma density, in contrast to an exponential distribution, is dependent on time elapsed, evolving from 0 at time zero to a steady state value. The time dependence of the probability of switching out of the grouped percept may therefore be complementary with previous descriptions. What is still missing from these theories, however, is the mechanism by which the perceptual state switches back and undergoes alternations; how do we account for switches out of the split percept, and the distribution of split durations?

Duration distributions are not well constrained by the trial average

The resilience of the alternating renewal process to capture the dynamics of buildup in a variety of circumstances, including those with duration-to-duration correlations likely carries the burden of overflexibility—for any given buildup function, a wide range of pairs of distribution functions may provide a good fit. We generated buildup functions using Monte Carlo as in figure 2 and used our analytical solution to find the gamma density parameters that minimized the squared error between the Monte Carlo and analytical buildup functions. In general, the parameters so found did not strongly fit the histograms of the duration samples used (see Figure ??). Specifically, whereas maximum likelihood confidence intervals estimated from the duration samples generated to construct short trials always contained the parameters to the gamma densities used in the Monte Carlo random number generators, the least squares estimates to the buildup function were only within the confidence intervals from the maximum likelihood estimates for 1 in 10 simulations.

However, for the special case when the both perceptual states have identical duration distributions, the parameter estimation for the gamma density functions from the buildup function is much better. This circumstance would occur when the inputs to the populations representing each percept are matched, e.g., when the stimulus is perfectly ambiguous. We generated buildup functions using Monte Carlo from two identical gamma densities, and found the single set of gamma parameters that minimized squared error between this and theoretical buildup function. For 1000 such simulations, 24.75% of the recovered parameters were within maximum likelihood confidence intervals, and in general the fits were much closer. For instances in which the original data (trial timecourses and durations) are unavailable, this method of estimation may prove useful for providing at least a rough estimate of the duration distributions underlying long-term dynamics.

What if the first percept is longer?

One issue we have not addressed so far in our presentation of the alternating renewal process model is inertia [?]. For ambiguous displays, the time until the first perceptual switch is typically much longer than subsequent durations of the same percept. For stimuli with

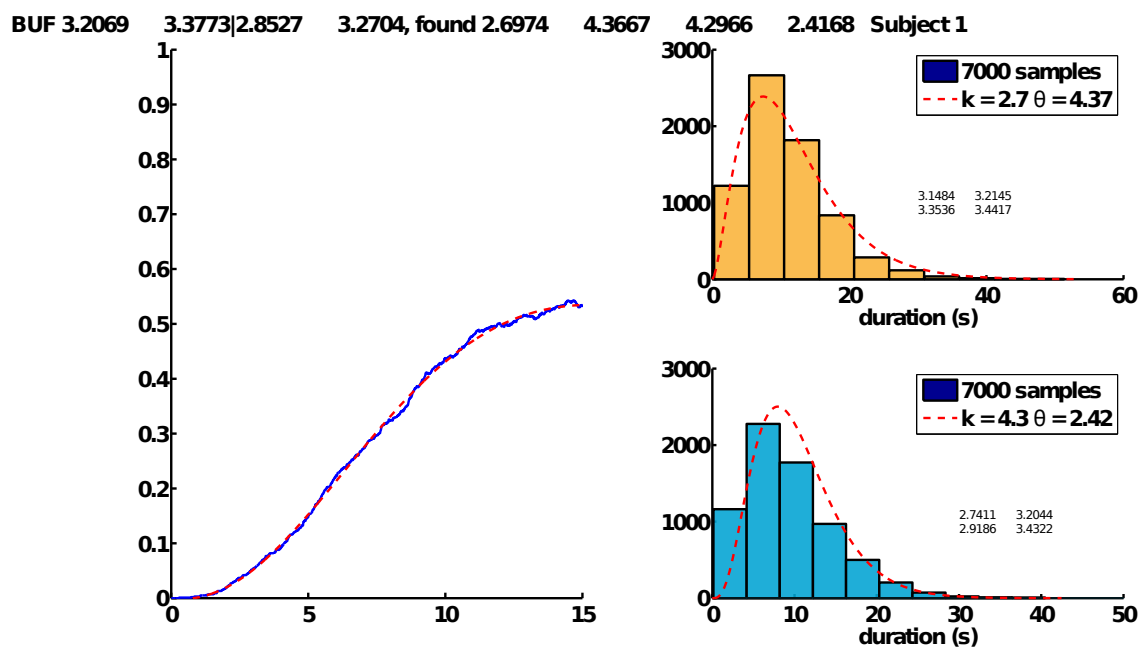


Figure 5

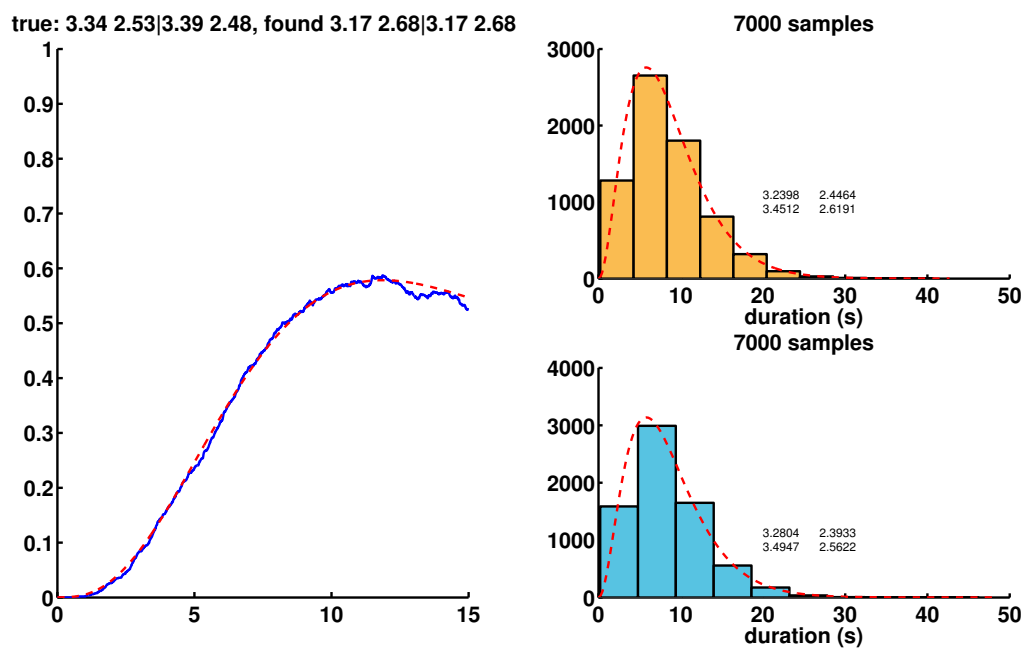


Figure 6: Better with 2 par model

ambiguous grouping, the distribution of initial grouped percept durations is different from other grouped percepts. Our theoretical model is capable of computing the buildup function from both steady state and initial percept distributions; however, this would introduce a third duration distribution, and increase the number of parameters to 6. For simplicity’s sake, we have only shown the 4 parameter model, which assumes that the initial percept duration is drawn from the same distribution as other grouped percept durations.

Our competition model, as it stands, produces a different distribution for initial and subsequent grouped percepts. However, the initial percepts are shorter in mean duration. This can probably be fixed by using a different set of initial conditions to achieve the correct initial dominance state— for instance, by setting the initial conditions so that the other population, that which represents the split percept, is highly adapted at the beginning of the trial. However, such an approach would be arbitrary, and leaves something to be desired in terms of explanatory value. What would be better is a more detailed model that captures elements of the sensory coding and neural dynamics that produce the perceptual states in the first place. For instance, percept formation might be subserved by neural populations that respond only to particular spectrotemporal input patterns. These encoding neural populations would be subject to adaptation, etc, and could allow us to make predictions about the perception of novel stimuli.

Our theoretical solution can be modified to account for experimental data in which the initial percept duration distribution is different from the steady state. However, there are circumstances in which inertia is fairly trivial, such as when buildup resets after a switch in attention [?]. Stationary distributions might be appropriate for such circumstances. We can take a more abstract view and consider a steady-state buildup function constructed from averaging over timepoints aligned by switches into the grouped percept.

Switch-triggered averaging produces steady state buildup function

To address the issue of inertia and the longer mean duration of the initial percept than subsequent grouped percepts on a trial, we explored a new method for constructing the buildup function: switch-triggered averaging. This method allows us to produce a buildup function from a single long trial. Ignoring the first and second percept duration, we constructed buildup functions by estimating the probability over time for the split percept based on an event-triggered average aligned to each switch into the grouped percept. This method produces a buildup function at steady state, the probability of perceiving the split organization not just from the beginning of the trial but rather from the beginning of any grouped percept duration over the course of a long presentation.

Methods

Competition model simulations

Competition model simulations followed the procedures reported previously in [6] for population firing rate model with spike frequency adaptation. Specifically,

$$\begin{cases} \dot{u}_1 &= -u_1 + f(-\beta u_2 - \gamma a_1 + I_1 + n_1) \\ \tau_a \dot{a}_1 &= -a_1 + u_1 \\ \dot{n}_1 &= \frac{-n_1}{\tau_n} + \sigma \sqrt{\frac{2}{\tau_n}} \eta(t) \\ \dot{u}_2 &= -u_2 + f(-\beta u_1 - \gamma a_2 + I_2 + n_2) \\ \tau_a \dot{a}_2 &= -a_2 + u_2 \\ \dot{n}_2 &= \frac{-n_2}{\tau_n} + \sigma \sqrt{\frac{2}{\tau_n}} \eta(t) \end{cases}$$

The variable u_1 corresponding to the short-time averaged firing rate of the population representing the “grouped” perceptual state, and u_2 the firing rate of the population representing the “split” perceptual state. The variables a_1 and a_2 represent the spike-frequency adaptation. Parameter γ controls the strength of the adaptation, and β controls the strength of suppression from the competing population. I_1 and I_2 are the external inputs driving the two populations, and n_1 and n_2 are independent Ornstein-Uhlenback noise generators with mean zero and variance σ , and a timescale of τ_n . The input-output function used was a sigmoid, with $f(x) = 1/(1 + \exp((x\theta)/k))$.

The simulation was carried out in nondimensionalized time, with the convention that one unit of time corresponds to 10 msec. Time constants given in simulation time units were $\tau_a = 200, \tau_n = 10$. The following parameter values are used: $k = 0.1, \theta = 0, \beta = 1$. The values of the external inputs to the populations I_1 and I_2 , the adaptation gain γ and the noise strength σ were varied as specified in the text, with the value of σ scaled in relation to the integration time step by $1/\sqrt{dt}$ to keep specified variance per unit time. Simulations were implemented in MATLAB using forward Euler integration with a time step of 0.1 (1 msec real time).

For each combination of parameter values, we simulated 500 trials of length 10 s with initial conditions $u_2(0), a_1(0), a_2(0), n_1(0), n_2(0) = 0$ and $u_1(0) = 0.5$; thus, at the beginning of each simulated trial, the first population to become dominant was always that corresponding to the first percept. With the resulting population firing rate timecourses, we obtained dominance durations by finding time points of the zero crossings of the differences of the firing rates. Using the samples of dominance durations obtained for each population (over 1000 durations for each population with each parameter set), we fitted gamma densities using maximum likelihood estimation. Simulated experimental buildup curves were constructed by averaging across trials the binary timecourse $u_2 > u_1$.

Derivation for alternating renewal process

In the alternating renewal process there are 2 random variables, $S(t)$ and $Z(t)$. $S(t)$ is the random elapsed time since last switching into the current state, evaluated at time t . $Z(t)$ is a dichotomous random variable, where $Z(t)$ in $0, 1$ codes for the percept, grouped or split. For sake of convenience, we introduce 2 probability density -mass functions: $f_0(s, t)ds = Pr\{S(t)\}$ in $(s, s + dt)$ and $Z(t) = 0$, and $f_1(s, t)ds = Pr\{S(t)\}$ in $(s, s + ds)$ and $Z(t) = 1$. The coupled pair of partial differential equations describing the evolution over time of these 2 probability density-mass functions is as follows:

$$\frac{\partial f_0}{\partial t}(s, t) = -\frac{\partial}{\partial s}(1 * f_0(s, t)) - h_{T_0}(s)f_0(s, t) \quad (1)$$

$$\frac{\partial f_1}{\partial t}(s, t) = -\frac{\partial}{\partial s}(1 * f_1(s, t)) - h_{T_1}(s)f_1(s, t) \quad (2)$$

where s is the elapsed time since entering state i and $h_{T_i}(s)$ is the hazard function, the probability per unit time of exiting the current state at time t . $h_{T_i}(s) = \frac{f_{T_i}}{\hat{F}_{T_i}}$, the ratio of the density function of durations T_i for state i and its complementary cumulative distribution function.

The value of $S(t)$ is reset to 0 whenever an alternation between states occurs. The initial flux of probability (a source) at $s = 0$ is determined by the probability of switches out of the previous state, leading to the following boundary conditions:

$$f_0(0, t) = \int_0^\infty h_{T_1}(s) f_1(s, t) ds \quad (3)$$

$$f_1(0, t) = \int_0^\infty h_{T_0}(s) f_0(s, t) ds \quad (4)$$

The probability that $Z(t) = 1, p_1(t)$, is the marginal probability mass function evaluated at $z = 1$. It is obtained by integrating $f_1(s, t)$ over all s ; and similarly for $Z(t) = 0$. We used the following initial conditions, corresponding to $Pr\{Z(t=0) = 1\} = 1$, and $Pr\{Z(t=0) = 0\} = 0$. In order to allow for a different distribution for the initial percept, we first solve for the case of beginning in state 1:

$$f_1(s, t=0) = \delta(s); f_0(s, t=0) = 0 \quad (5)$$

For sake of simplifying notation, we define $p_{1|1}(t) = Pr\{Z(t) = 1|Z(t=0) = 1\}$. Using these conditions yields the following solution:

$$p_{1|1}(t) = \tilde{F}_{T_1}(t) + \frac{1}{2\pi} \int_{-\infty}^\infty dw \frac{1}{i\omega} \left[\hat{\tilde{F}}_{T_1}(\omega) \hat{f}_{T_0}(\omega) \hat{f}_{T_1}(\omega) \frac{i\omega}{1 - \hat{f}_{T_0}(\omega) \hat{f}_{T_1}(\omega)} \right] e^{i\omega t} \quad (6)$$

where $\hat{f}(x)$ is the Fourier transform of $f(x)$

To find the probability that $Z(t) = 1$, given $Z(t=0) = 0, p_{1|0}$, we time shift the above expression by the durations of the initial state, T_0^0 , whose density function is $p_{T_0^0}(t)$ [changed f to p]. This amounts to a convolution of the density for initial durations (and first switch times) with the previous solution:

[again changed f to p]

$$p_{1|0}(t) = \int_0^t f_{T_0^0}(s) f_1([t-s]|z(0)=1) ds \quad (7)$$

Thus the solution can be given in the Fourier domain as:

$$\hat{p}_{1|0}(\omega) = \hat{f}_{T_0^0}(\omega) \hat{p}_{1|1}(\omega) \quad (8)$$

Using the simplifying assumption that $f_{T_0^0}(t) = f_{T_0}(t)$, that is, that the initial percept duration is from the same density function as all other T_0 , we find:

$$\hat{f}_{1|0}(\omega) = \hat{\tilde{F}}_{T_1}(\omega) \left(\hat{f}_{T_0} + \frac{\hat{f}_{T_0}^2(\omega) \hat{f}_{T_1}(\omega)}{1 - \hat{f}_{T_0}(\omega) \hat{f}_{T_1}(\omega)} \right) \quad (9)$$

At $\omega = 0$, $\hat{f}(\omega) = \mu(T_1)/(\mu(T_1) + \mu(T_0))$. From here, the expression in the time domain is obtained by taking the inverse Fourier transform and finding the integral from 0 to t.

Monte Carlo simulations

We used Monte Carlo methods to test the analytical solution above, and to evaluate its performance in relating the buildup function to the underlying distributions of dominance durations.

To generate a wide range of plausible buildup functions, we simply specify two distributions with random parameters within the bounds [1,4]. These were decided upon arbitrarily after visual inspection of many uniformly generated buildup Monte Carlo buildup functions. One of these distributions is labelled as the grouped percept durations, and the other as the split percept durations. For a given simulated

trial timecourse, we draw alternating random samples from each of these two distributions. We begin with the distribution corresponding to the grouped state, and continue drawing samples until the sum of all the durations exceeds the length of a trial. These trial durations are converted into discretized timecourses by assigning a value of 0 to time intervals during which the state corresponds to a grouped percept, and assigning a value of 1 to the time intervals for which the percept state was split. In Monte Carlo, we produce 1000 such trial timecourses, then take the average at each time point.

To estimate the gamma parameters from these Monte Carlo generated buildup functions, we used the analytical solution (above) and searched for the 4 parameters that minimized the squared error between the analytical and the Monte Carlo generated buildup function.

All simulations were implemented in MATLAB. Maximum likelihood estimation was carried out using the gamfit function from the stats toolbox.

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