An alternating renewal process describes the buildup of perceptual segregation

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**Abstract**

Some ambiguous scenes present a perceptual tension between integration and segregation. From an initial perceptual organization in which different stimulus features are integrated, the percept may suddenly differentiate, and those features separate into distinct representations. For example, the segregation of acoustic features into different streams can take several seconds to occur. For long presentations, perception may alternate between integration and segregation. In behavioral experiments, when a subject’s reports over time of experiencing a split perceptual state are averaged over repeated trials, one obtains a buildup function, a smooth timecourse for the probability of segregation. The buildup function has been said to reflect some underlying mechanism of evidence accumulation or adaptation. We present a statistical model from the framework of an alternating renewal process that generates buildup functions without an accumulative process. In our model, an observer’s perception over a trial alternates between each state, with random and independent durations composed of samples from percept-specific probability density functions. Using this theory, we describe the short-term dynamics observed on short trials in terms of the long-term statistics of percept durations for the two alternating organizations. We generated simulated buildup functions using pseudo-mechanistic models of mutually inhibitory percept-selective neural populations widely used to characterize perceptual bistability, which our statistical-dynamics model describes well, even when the simulated durations show history dependence through slow adaptation. We propose that accumulation is not a necessary feature to produce buildup. Generally, any physical or model system that undergoes dichotomous state switching approximating a renewal process with two independent density functions will have a buildup function that can be predicted solely on the basis of those density functions.

1. **Introduction**

For some stimuli in the auditory and visual modalities with ambiguous grouping cues, the probability of perceptual “splitting” increases with time, and subjects report experiencing alternations between grouped and split perceptual organizations. For example, a widely used paradigm in auditory stream segregation uses the two-tone triplet stimulus, ABA-ABA-… (van Noorden, 1975), where A and B refer to tones at different frequencies, and - represents a silent interval. Depending on the relative tone-frequency and presentation rate, listeners may be more likely to report perceiving either triplet patterns grouped into a galloping rhythm, or two segregated streams: A-A… and B---B… (Figure 1). Studies using ambiguous ABA- tone sequences have shown that perceptual splitting of sound events with different acoustic features increases over time (Anstis and Saida, 1985; Bregman, 1978; Cusack et al., 2004). There is typically a period of time over which the probability of the segregated percept increases, starting from the initiation of a presentation (Anstis and Saida, 1985; Bregman, 1978) or a switch in the focus of attention (Cusack et al., 2004). A similar phenomenon has been reported in the visual modality. When viewing ambiguous dynamic plaids constructed from two drifting gratings at intermediate speed and angle, observers have reported first experiencing coherent motion of a unified plaid pattern, even when, in the long term, their perception is biased towards transparent motion of the individual gratings in each of their component directions (Rubin and Hupé, 2004). The change in probability of observers reporting a split perceptual organization over time can be quantified as a buildup function. This can be stated quantitatively as , where Z(t) = 0 indicates a grouped perceptual organization at time t and Z(t) = 1 indicates a split perceptual organization. The psychophysical data show that such dynamically changing perceptual states are accompanied by reports of perceptual alternations over long presentations (Deike et al., 2012; Pressnitzer and Hupé, 2006); the buildup function approaches a steady state value that equals the fraction of time that the split organization is dominant.

Such perceptual dynamics are of great interest in audition because they likely involve the same mechanisms that enable listeners to perceptually organize the individual sound sources in a complex auditory scene, a process known as stream segregation. Various quantitative descriptions of the buildup function invoke proposed mechanisms of stream segregation. One theoretical explanation for the perceptual organizations observed with the ABA- stimuli is grouping by coactivation (for a review, see Carlyon (2004)). Sound signals that excite the same population of neurons are grouped, whereas those that activate separate populations are perceived as coming from separate sources, that is, split. Some theories (Bee et al., 2010; Micheyl et al., 2005; Pressnitzer et al., 2008) propose that the buildup function reflects the accumulation of adaptation over seconds, or multi-second habituation, which leads to a decrease over time of activation by the other tone of auditory neurons tuned to each of the two tone frequencies.

The accumulation-based account of the buildup function has produced neurometric models that can quantitatively predict the switch from the grouped to the split percept; however, it is unable to account for how subjects undergo continued switches between perceptual organizations. We bypass the mechanistic issue and show that the buildup function can be described well and quite generally by a statistical model that ignores accumulation. The gradual increase in probability of a split percept over time could reflect the dynamics of an entirely random underlying switching process with a given initial state. The long-term dynamics of perceptual bistability consist of alternations between mutually excusive percepts. The duration histogram of each percept has been well-fit by a gamma density (Pressnitzer and Hupé, 2006; Shpiro et al., 2009). We believe that the short-term increase in probability of split percepts, observed when short trial perceptual timecourses are averaged, could reflect the dominance duration distributions observed over long trials. To test this idea, we use the theoretical framework of an alternating renewal process. We use the fitted gamma densities for the dominance durations, without consideration for history dependence between successive durations, to account for the experimentally measured buildup function for a stimulus with ambiguous grouping, in models and experiments. The statistical model is general and based on the following underlying assumptions: 1) the perceptual state alternates back and forth between grouped and split; 2) the durations for these perceptual epochs are random, independent and stationary; and 3) the initial percept on for a given presentation is always the grouped percept.

In addition, we adapted existing neuro-mechanistic computational models frequently used to characterize perceptual bistability to produce buildup functions, in order to explore how different mechanisms of alternation affect buildup functions so produced, as well as the performance of our statistical model in describing them.

1. **Materials and m**eth**ods**

To compute a buildup function empirically, one averages over many trials the timecourse of a random binary state variable (see Figure 2a, 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. This constitutes an alternating renewal process (for a review of renewal theory, see (Cox, 1962).

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 state durations, and the other to the split state durations. These gamma distributions were specified randomly with parameters within the bounds [1,5]. These bounds were decided upon after visual inspection of many Monte Carlo simulated buildup functions, for sake of simplicity. We draw the first sample from the distribution corresponding to the grouped state, the second from that corresponding to the split state, and continue drawing samples from each distribution in alternation until the sum of all the durations exceeds the specified length of a trial. These trial durations were converted into discretized timecourses by assigning a value of 0 or 1 to time intervals during which the state corresponds to a grouped or split percept, respectively. In Monte Carlo simulations, we produce an arbitrarily large (1000 trials) number of such timecourses, and then take the average at each time point. This gives a relative frequency estimate of , i. e., the mean of

We have used a population density approach similar to that used in Stinchcombe et al. (2012) for modeling stochastic gene expression to characterize the buildup function. This formulation allows us to solve for the buildup function analytically. 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 percept durations. This theoretical solution coincides with the Monte Carlo simulation results (see Figure 2b). This is convenient, as the analytical solution is computationally less expensive than iterative Monte Carlo simulations, and the solution is exact.

We wanted to test whether it was possible to recover the parameters for the long-term statistics of dominance durations from the buildup function. To estimate the gamma parameters from Monte Carlo generated buildup functions, we used the analytical solution (below) and searched for the 4 parameters that minimized the sum of the squared errors between the analytical and the Monte Carlo generated buildup function. We also tested a constrained model that assumes that the duration distributions for grouped and split percepts are matched. All simulations were implemented in MATLAB.

## Solving analytically for the alternating renewal process

In the alternating renewal process we consider a population of random time courses, in which 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, respectively. The following equations are roughly analogous to those used in population analysis. Exits from the current state, like deaths, are carried by the hazard terms, and births or entries into a state are carried by the boundary conditions as s=0. For a review, see Cox (1962) For sake of convenience, we introduce 2 probability mass functions:

and

where is the elapsed time since entering state , and is the hazard function, the probability per unit time of exiting the current state at time , given in state . The hazard function for state is defined as , the ratio of the density function of durations and its complementary cumulative distribution function, . We used the gamma probability density function, which has shape and scale parameters, and , respectively. The general form is . For integer shape parameter, this function becomes , and the hazard function is given by

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

The probability that , is the marginal probability mass function evaluated at . It is obtained by integrating over all s; and similarly for . We used the following initial conditions, corresponding to , and . In some experimental contexts, it has been observed that the first percept duration for an ambiguous stimulus is longer than subsequent durations (see Discussion). In order to accommodate for this possibility, we first solve for the case of beginning in state 1:

For the sake of simplifying notation, we define .

These partial differential equations are linear but coupled. By taking the Fourier transform, all convolutions become products, yielding the following solution:

where   is the Fourier transform of .

To find , the probability that , given , we time shift the above expression by the durations of the initial state, , whose density function is (t). This amounts to a convolution of the density for initial durations (and first switch times) with the previous solution:

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

Using the simplifying assumption that , that is, that the initial percept duration is from the same density function as all other , we find:

At , . From here, the function in the time domain is obtained by taking the inverse Fourier transform and finding the integral from 0 to .

## Competition model simulations

We chose to use a competition model as a test-bed for the theory of the alternating renewal process for different dynamical regimes of perceptual alternation- in particular, for noise-driven switches, for which correlation between successive dominance durations is low, and for adaptation-driven switching, in which correlation is high. We chose to use existing observer models for perceptual bistability to produce buildup functions to see if we could relate these to the underlying dominance durations using renewal theory. Previous investigations (Laing et al., 2010; Pastukhov et al., 2013; Shpiro et al., 2009; Wilson and Cowan, 1972; Wilson, 2003) have 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. They make inhibitory connections onto one another, so the population with the highest firing rate typically dominates the other (Figure 5a). 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 (Pastukhov et al., 2013; Shpiro et al., 2009) and triplets with streaming integration/segregation (Mill et al., 2013).

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 activity of 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 brain appears to be a very noisy system, with random fluctuations occurring at multiple scales such as vesicular release and spiking variability. The competition models with attractor dynamics, in which switching between dominance epochs is driven by noise, appear to be more consistent with the statistics of dominance durations observed in psychophysical experiments (Shpiro et al., 2009), and we exploit the fact that the models operating within this regime produce buildup functions that are consistent with those measured experimentally.

Competition model simulations followed the procedures reported previously in Shpiro et al. (2009) for population firing rate model with spike frequency adaptation. Specifically,

The variable corresponds to the short-time averaged firing rate of the population representing the “grouped” perceptual state, and to the firing rate of the population representing the “split” perceptual state. The variables and represent the spike-frequency adaptation. Parameter γ controls the strength of the adaptation, and β controls the strength of suppression from the competing population. and are the external inputs driving the two populations, and and are independent Ornstein-Uhlenback noise generators with mean zero and variance σ, and a timescale of . The input-output function used was a sigmoid, with .

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 = 200, = 10. The following parameter values are used: = 0.1, θ = 0, β = 1. For attractor dynamics, we set the value of the external inputs to populations and to 0.6, the adaptation gain γ to 0.1, and the noise strength σ to .12. For oscillation dynamics, we set the value of the external inputs to populations and to 0.6, the adaptation gain γ to 0.3, and the noise strength σ to .09. The value of σ was scaled in relation to the integration time step by 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).

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 a very simple manner (see Figure 5), by setting the initial condition on the population representing the grouped percept to half its maximum value. For each combination of parameter values, we simulated 500 trials of length 20 s with initial conditions , , , , and ; thus, at the beginning of each simulated trial, the first population to become dominant was always that corresponding to the grouped percept. Simulated experimental buildup curves were constructed by computing the average for each time point across trials of the binary timecourse .

We obtained dominance durations by finding time points of the zero crossings of the differences of the firing rate timecourses. 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 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. We compared the simulated empirical buildup functions with those predicted under our statistical model using these fitted gamma parameters by computing , the coefficient of determination.

1. **Results**

## Monte Carlo simulated and analytically computed buildup functions converge, but duration distributions are not well constrained by the buildup function

We propose that the buildup function arises from a system that alternates between two states from a known starting state, and that the dwell times in each state are independent with durations drawn from two probability density functions. Using renewal theory, we found an analytical solution that relates the buildup function to the density functions describing the state durations. We also performed Monte Carlo simulations to generate random samples from two probability density functions with parameters and , construct simulated trials from these samples, and compute buildup functions (Figure 2). The statistical model uses the 4 parameters of the duration density functions to make a prediction for the buildup function under an alternating renewal process, and the Monte Carlo simulated buildup functions converge with this prediction.

Because we have an expression in closed form, it should be possible not only to predict the buildup function from the gamma density parameters describing the durations in each state, but also to predict the gamma density parameters from the buildup function. We generated buildup functions using Monte Carlo simulations as above, and used our analytical solution to recover the gamma density parameters that minimized the squared error between the analytical and simulated buildup functions (Figure 3). In general, the parameters so found did not describe well the duration samples that had been generated to produce the simulated buildup function. Specifically, we used one-sample Kolmogorov-Smirnov tests to determine whether the duration samples came from the gamma distribution obtained from the least squares fit of our 4-parameter statistical model to the simulated buildup function. Only 24.5% of simulations produced good fits, and the average KS distance between sample and the fitted distribution was .09.

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 occurs in competition model simulations 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 simulations from two identical gamma densities, and found the single pair of gamma parameters that minimized squared error between this and theoretical buildup function (Figure 4). For 1000 such simulations, 63% of the recovered parameters were indistinguishable from the sample empirical distribution by Kolmogorov-Smirnov tests, and in general the fits were much closer, with a mean KS distance of .04. This method of estimation may prove useful for providing at least a rough estimate of the duration distributions underlying steady state switching dynamics.

## Competition model simulations produce buildup functions consistent with an alternating renewal process, even when trial timecourses violate assumptions

We used pseudo-neuronal competition models to produce experimental timecourses similar to those reported in the psychophysical literature on ABA- tone sequences. Our statistical model makes three assumptions describing an alternating renewal process: the initial state is always the same, the state alternates back and forth, and the state durations are random, independent and stationary. By setting the initial conditions to ensure that the population representing the grouped percept was always active first, we were able to satisfy the assumption that the initial perceptual state is fixed. The competition models also satisfy the assumption of alternation between perceptual states of grouped and split. However, the state durations are not necessarily independent—depending on the dynamical regime in which the competition model is operating, attractor or oscillator, there can be significant history dependence between state durations.

The difference between oscillator and attractor dynamics in these competition models is most simply understood by observing how the system would behave without noise (Moreno-Bote et al., 2007; Shpiro et al., 2009). For oscillation dynamics, 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 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 is caused by the noise itself.

When the switches between perceptual states are driven by noise, as under attractor dynamics, correlations between successive dominance durations are low (). An example trial timecourse is shown in Figure 5b, top. By averaging over many trials the dominance state , we obtain a simulated empirical buildup function. We fitted gamma parameters to the dominance durations, and used these parameters to generate analytical buildup functions using the alternating renewal process model (Figure 5b, bottom). The prediction of buildup function for an alternating renewal process with the underlying duration distributions with those fitted gamma parameters very strongly fits ( = 98%) the buildup function obtained empirically by averaging over many trials.

## Oscillation dynamics produces buildup functions that dramatically differ from those previously reported in psychophysical experiments

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 (Shpiro et al., 2009). The mean and circular variance of dominance durations under these dynamics 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 (Pressnitzer and Hupé, 2006).

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 indicate that the buildup function is monotonic. To our knowledge, no psychophysical experiments have shown a buildup function timecourse with a damped oscillatory approach to steady state. Buildup functions produced under oscillation dynamics in our competition model (Figure 6), however, display damped oscillations reflecting the underlying periodicity of the mechanism of alternation from the oscillator regime. These buildup functions are derived from perceptual timecourses for which there are significant correlations between successive percept durations, such that the present perceptual state depends on the cumulative history of previous percepts. Although the correlation coefficient between durations of subsequent percepts was significant ( = 0.28), the fit to the buildup function by finding the parameters of density functions for long term percept durations was strong ( = 93%). Despite ignoring history dependence, the theory linking the transient dynamics described by buildup function to steady state dynamics gives accurate predictions. Because of the underlying periodicity of the oscillator, the gamma density functions look more like delta functions—the dominance durations are not highly variable, and so switches are more likely to occur at similar times on different trials. This is why those gamma density functions produce buildup functions that look like damped oscillations.

1. **Discussion**

During presentations of ambiguous stimuli subjects may perceive switching between integration and segregation. For short presentations (i. e., 10 second trials, as in Pressnitzer et al. (2008), Micheyl et al. (2005)), there may be only a few switches after the initial percept—in the van Noorden ABA- paradigm discussed in this paper, the initial percept is typically integration— but for long presentations (i. e., 4 minute trials as in Pressnitzer and Hupe (2006), Denham et al. (2010)), haphazard alternations typically occur. We introduced and explored a statistical model for the buildup function, the probability versus time of segregation. Our model accounts for the buildup function as the mean over trials in the short presentation case, or the switch-triggered average time course for long runs (see below), in terms of an alternating renewal process (ARP). By definition a renewal process has no memory about the duration of the preceding percept; there are no correlations between successive percepts, consistent with reports from behavioral experiments (Pressnitzer & Hupé, 2006). The model contains no explicit description for an accumulative or adaptive mechanism.

The buildup function for our ARP model can be computed with Monte-Carlo simulations or it can be evaluated with the analytical solution (in terms of Fourier transforms) of the partial differential equations for the probability mass functions (eqns xxx) in the two states. In this direct framework, one assumes that the duration distributions for the two percepts are known, under stationary switching, say, for long runs. For our case studies we assume gamma distributions, as they are often applied and fitted to behavioral data for bistable perceptual dynamics. To restate, the model enables one to understand and predict from the stationary statistics the system’s transient behavior – the buildup function given a specified initial state. From a dynamical systems point of view, it seems surprising to predict transients from knowledge of a steady state only. In our case of a two-state switching system, with renewal, the two residence time distributions contain all the information that is needed. We applied the ARP model, in this direct mode, to predict buildup functions for neuronal-like competition models. The predictions compared well with the simulated empirical buildup functions for examples of monotonic buildup (as typically reported from experiments) as well non-monotonic (damped oscillatory) buildup time courses.

For the converse case, the indirect framework, we ask about predicting the long time behavior from the early transient of buildup. For short presentations, but adequately long for 2-3 switches to occur one may still apply the ARP model. If there are enough trials to estimate well the percept-duration distributions then one can predict the full time course including the long time average behavior, as well as the expected switch-triggered average time course. However, if the presentations are so brief that on average 1 or fewer switches occur during buildup, then application of the ARP model is problematic especially since for some stimuli the initial percept duration may be significantly longer than subsequent durations (see below).

## 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 (Hupé and Pressnitzer, 2012). For ambiguous displays, the time until the first perceptual switch is typically much longer than subsequent durations of the same percept. For stimuli with ambiguous grouping, the distribution of initial grouped percept durations is different from other grouped percepts. In some experimental data collected with short trials, this might not be especially concerning– most trials contain one or fewer switches, i. e., from the integrated to the segregated percept. With these data, the distribution of initial switch times would be sufficient to describe a renewal process accounting for buildup. For data collected from longer trials with many alternations, however, it might be desirable to distinguish between initial and subsequent grouped percept durations. 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.

To adequately explain these perceptual dynamics with a physiological model, there should be some description of the sensory coding mechanisms that underlie the formation of perceptual organization. The specific mechanisms for switching in human stream segregation may be complex; Kondo and Kashino (2009) find that feedforward and feedback processes in a thalamocortical loop might be differentially engaged for switches into and out of the perceptual organization that is strongest. The renewal process model is agnostic to the specific mechanism by which states are found and alternations occur; we have used existing competition models for the sake of illustration and as a computational test-bed. Similar competition-like processes have been used to explain the alternations observed in ambiguous motion (Pastukhov et al., 2013) and stream segregation (Mill et al., 2013) experiments. A better understanding of the characteristics of the neural populations on the encoding side of perceptual organization could enable us to more accurately model the psychophysical data.

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 (Denham et al., 2010). 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.

To address the issue of inertia and the longer mean duration of the initial percept than subsequent grouped percepts on a trial, we propose 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. Discarding the first and second percept duration, we can construct 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 switch into the grouped perceptual organization over the course of a long presentation.

## Do correlations between successive perceptual state durations matter for describing buildup functions?

The competition model simulations presented here provide a test-bed for our novel statistical model. When dominance durations are not statistically independent, and there is history dependence between successive perceptual epochs, will modeling the buildup function as an alternating renewal process with state durations from underlying independent gamma densities still provide a good description? We measured the correlations in the data produced for both a noise-driven and adaptation-driven alternation dynamics. As previously described, the adaptation-driven perceptual timecourses showed moderate correlations between the durations of successive percepts. Our statistical model, however, ignores this history dependence entirely, treating percept durations as independent random variables described by their probability density functions. The buildup functions so computed matched the buildup function computed from the output of the neuronal competition models. Correlations between subsequent perceptual epochs do not need to be taken into consideration to predict the buildup function; rather, these perceptual dynamics are described sufficiently well by the underlying distributions of dominance durations.

Previous computational approaches to describing the buildup function (Micheyl et al., 2005; Pressnitzer et al., 2008) have pointed to the accumulation of adaptation as a critical feature for the increase over time in the probability of a split percept. Multi-second habituation in the auditory periphery (Pressnitzer et al., 2008) can predict the buildup function obtained through psychophysics. It may therefore be surprising that the alternating renewal process neglects to account for adaptation. We believe that previous approaches and our own can be reconciled, and may even be complementary. The choice of gamma densities to generate dominance durations implicitly invokes adaptation (Wilbur and Rinzel, 1982). This is because the hazard function for a gamma density, in contrast to an exponential distribution, is dependent on the time elapsed, evolving from 0 at time zero to a steady state value. The time dependence of the probability of switches from the grouped to the split perceptual organization may therefore be seen as complementary with the habituation-based explanation for the buildup function.

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? Our statistical model is agnostic to the mechanism of switching, but it does use information about alternations to predict perceptual dynamics. This is a novel insight linking transient dynamics to any underlying steady state process generating alternations, and produces surprisingly good predictions with minimal assumptions.

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1. **Figure legends**

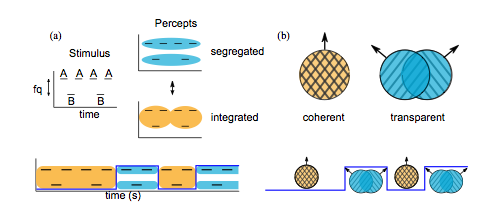
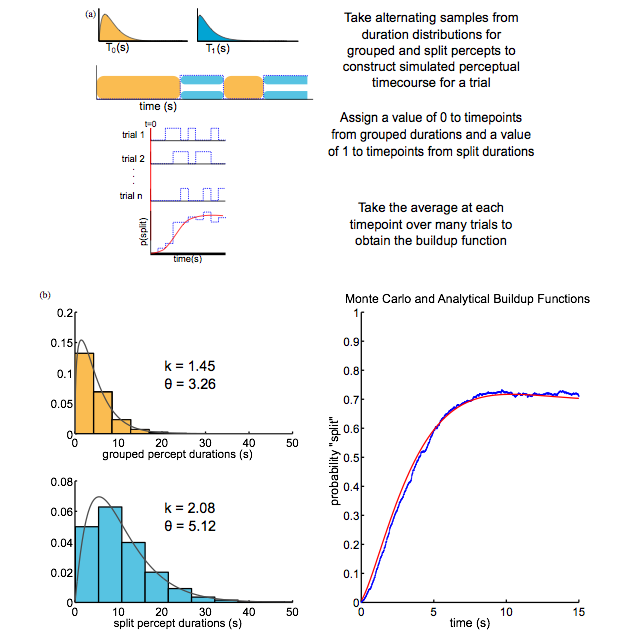
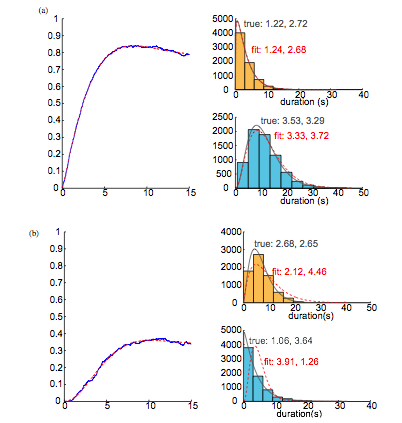
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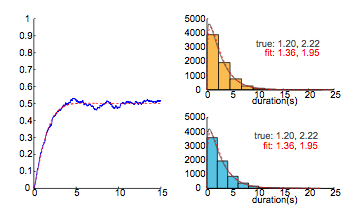
Figure 1: Examples of stimuli that can produce ambiguous grouping. (a) Van Noorden triplets with ambiguous stream segregation. Listeners report alternations between hearing integration (bottom, orange) and segregation (top, blue) of the component tone frequencies. (b) Moving gratings at certain angles can produce ambiguous motion. Observers report alternations between coherent and transparent motion of the component gratings.



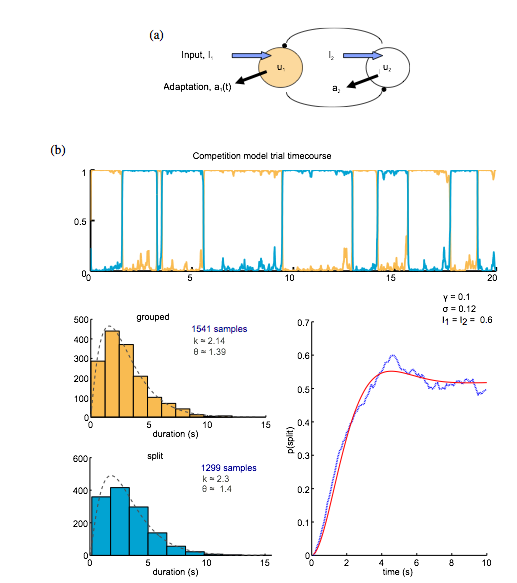
**Figure 2:** (a) Visualization of the alternating renewal process producing a buildup function. We used gamma probability density functions approximating duration distributions to construct Monte Carlo simulations. The analytical solution to the alternating renewal process model, shown as a red solid curve (bottom), allows us to predict the buildup function solely from the distributions of dominance durations of each of the perceptual states. (b) Monte Carlo simulation 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).



**Figure 3:** We generated buildup functions, shown in blue, with Monte Carlo simulations from known gamma densities (shown in gray on the histograms). We then obtained estimates for those parameters by finding the least squares fit to the Monte Carlo simulated buildup functions from our four parameter analytical expression. The fitted buildup function and the gamma densities so recovered are shown in dashed red lines. (a) A successful recovery of the gamma density parameters from the buildup function. (b) A case in which the parameters that minimize squared error between the analytical and the Monte Carlo simulated buildup function do not match the underlying gamma densities used to produce it.



**Figure 4:** The same as Figure 5, except that the Monte Carlo simulations have been constrained so that the gamma densities for each of the two states are matched. In addition, the least squares fit requires finding only two parameters. The recovered parameters for the duration distributions usually match those used to generate the Monte Carlo simulated buildup function.



**Figure 5**: (a) Mutual inhibition population firing rate model producing buildup. We choose initial conditions to ensure that the population representing the grouped percept, u1, is always dominantat 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. We simulated 500 trials to produce the buildup function, lower right (blue). Histograms of the dominance durations, with maximum likelihood estimated gamma density parameters and the associated density functions (gray), are shown in the lower left. These parameters allow us to compute analytically the resulting buildup function for an alternating renewal process (red). The buildup function looks similar to those reported in the psychophysical literature, and the statistical model’s prediction is good (R-Squared = 98%)**.**

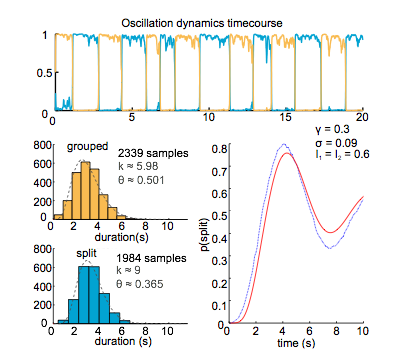


Figure 6: Competition model simulation results for model parameters that produce oscillation dynamics with adaptation-driven switching. Top, population activity timecourse for one 20-second trial. The dominance durations are much more regularly timed than those produced under attractor dynamics, reflecting the clock- like periodicity of the underlying oscillator. These oscillations are dramatically present in the average over 500 simulated trials, lower right (blue). To our knowledge, no such buildup functions have been observed psychophysically. The maximum likelihood estimated gamma density parameters are shown in the lower left (gray), and the analytically computed buildup function for an alternating renewal process with those parameters is shown in the lower right (red). The fit between the analytical solution and the trial average is still quite good (R-squared = 93%).

1. **Supplementary Material**

Please submit any data, information, figures, or tables that are not part of the main text of the article, as supplementary material.

The Supplementary Material can be uploaded as Data Sheet (word, excel, csv, fasta, pdf or zip files), Presentation (power point, pdf or zip files), Audio (mp3, wav or wma) or Movie (avi, divx, flv, mov, mp4, mpeg, mpg or wmv). The supplementary material is not typeset so please ensure that all information is clearly presented, includes an appropriate caption, and that the style conforms to the rest of the paper.

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