

From one to many (and back again): an alternating renewal process  
describes the buildup of perceptual segregation

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13

14 Abstract

15 For some ambiguous scenes, perceptual organization becomes more complex as a subject's  
16 presentation time increases, in that different stimulus features are gradually more likely to be grouped  
17 into different perceptual representations. In particular, the segregation of acoustic features into  
18 different streams takes time to build up. We compute the buildup function for a particular stimulus as  
19 the probability as a function of time that subjects report experiencing a split perceptual organization.  
20 Previous approaches to characterizing the buildup function relate the current perceptual state to some  
21 underlying mechanism of accumulation, of, for instance, adaptation. We present a statistical model

from the theoretical framework of an alternating renewal process that produces buildup functions in the absence of any accumulative process. In this statistical model, the observer alternates between perceptual organizations, as in perceptual bistability, with dominance durations composed of random samples from independent density functions. Using this theory, we can describe the short-term dynamics of buildup observed on short trials in terms of the long-term statistics of percept durations for the two alternating perceptual organizations. This model performs well in describing buildup functions computed from pseudo-neuronal simulations of neural populations with competition architecture that undergo alternations. Depending on the parameters, these competition model simulations sometimes produce history dependence through accumulation of adaptation. Nonetheless, our switching model, which neglects history dependence from accumulative processes, is able to predict the buildup function. This indicates that accumulation is not a necessary feature to produce or to describe a buildup function. Rather, any model producing buildup will have an underlying alternating renewal process, the statistics of which are sufficient to account for buildup.

35

## 36 1. Introduction

37 For some stimuli in the auditory and visual modalities with ambiguous grouping cues, the probability  
38 of perceptual “splitting” increases with time. One example of this is found in auditory stream  
39 segregation, using an ABA- stimulus (van Noorden (1975)). A and B refer to tones at different  
40 frequencies, and - represents a silent interval. Depending on the difference in frequency and  
41 presentation rate of the tones, listeners might be biased to hear grouped triplet patterns integrated into  
42 a galloping rhythm, or segregated streams of tones at separate frequencies (Figure 1). A number of  
43 studies using ambiguous ABA- tone sequences (van Noorden (1975)) have shown that perceptual

44 splitting of sound events with different acoustic features increases over time (Bregman (1978); Anstis  
45 and Saida (1985); Cusack et al. (2004)). There is typically a period of time over which the probability  
46 of the segregated percept increases, starting from the initiation of a presentation (Bregman (1978);  
47 Anstis and Saida (1985)) or a switch in the focus of attention (Cusack et al. (2004)). In addition, a  
48 similar phenomenon has been reported in the visual modality. When viewing ambiguous moving  
49 plaids constructed from two moving square wave gratings at intermediate speed and angle, observers  
50 have reported first experiencing coherent motion of a unified plaid pattern, even when, in the long  
51 term, their perception is biased towards transparent motion of the individual gratings in each of their  
52 component directions (Rubin and Hupe (2004)). The change in probability of observers reporting a  
53 split perceptual organization over time can be quantified as a buildup function. This can be stated  
54 quantitatively as  $p(z(t) = 1|z(0) = 0)$ , where  $z(t) = 0$  indicates a grouped perceptual organization at  
55 time  $t$  and  $z(t) = 1$  indicates a split perceptual organization. The psychophysical data show that such  
56 dynamically changing perceptual states are accompanied by reports of perceptual alternations (Deike  
57 et al. (2012)). Because of the ambiguity of the stimuli, subjects report experiencing sudden switches  
58 between one perceptual state and the other (Pressnitzer and Hupé (2006); Hupé and Pressnitzer  
59 (2012)) over long presentations, even after the buildup function has reached steady state.  
60

61 In the auditory domain, these perceptual dynamics have been a subject of great interest because it is  
62 thought to be a product of the same mechanisms that enable listeners to perceptually group  
63 components of an acoustic signal according to the sources that produced them, a process known as  
64 stream segregation. Many explanations of buildup appeal to proposed mechanisms of stream  
65 segregation. One theoretical explanation for the perceptual organizations observed with the ABA-  
66 stimuli is grouping by coactivation (for a review, see Carlyon (2004)). Sound signals that excite the  
67 same population of neurons are grouped, whereas those that activate separate populations are

68 perceived as coming from separate sources, that is, split. Some theories (Micchely et al. (2005);  
69 Pressnitzer et al. (2008); Bee et al. (2010)) propose that the buildup function reflects the  
70 accumulation of adaptation over seconds, or multi-second habituation, which leads to a decrease over  
71 time of activation by the other tone of auditory neurons tuned to each of the two tone frequencies.

72

73 The accumulation-based account of the buildup function can quantitatively predict the switch from  
74 the grouped to the split percept; however, it is unable to explain why subjects undergo continued  
75 switches between perceptual organizations. We show that the buildup function can be described well  
76 by a model that uses the statistics of alternations, but no accumulation. The gradual increase in  
77 probability of a split percept over time could reflect the dynamics of an entirely random underlying  
78 alternating renewal process with a given initial state. The long-term dynamics of perceptual  
79 bistability consist of alternations between mutually exclusive percepts. The duration histogram of  
80 each percept is well-fit by a gamma density (Shapiro et al. (2009); Pressnitzer and Hupé (2006)). We  
81 believe that the short-term increase in probability of split percepts, observed when short trial  
82 perceptual timecourses are averaged, could reflect the dominance duration distributions observed  
83 over long trials. To examine this relationship we use the theoretical framework of an alternating  
84 renewal process. In this investigation we show that these distributions of percept durations, without  
85 consideration for history dependence between successive durations, can account for the  
86 experimentally observed perceptual dynamics for a stimulus with ambiguous grouping, as follows:

87

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

91

92 In addition, we use existing computational models of perceptual bistability to explore how different  
93 mechanisms of alternation affect the model's behavior with regard to the buildup function.

94

95 **2. Materials and methods**

96 The process of computing the buildup function empirically involves the averaging over many trials of  
97 the timecourse of a random binary state variable (see Figure 2a, blue lines). In our statistical model,  
98 the initial state (percept) is fixed, but the dwell time in this state is a random variable characterized by  
99 its probability density function. Subsequently the system switches randomly between two states, each  
100 of which has its own fixed duration distribution. This constitutes an alternating renewal process.

101 We initially tested this theory in Monte Carlo simulations by simply constructing *in silico* perceptual  
102 timecourses according to the above assumptions (see Figure 2, (a)). For a given simulated trial  
103 timecourse, we draw alternating random samples from each of two distributions— one corresponding  
104 to the grouped state durations, and the other to the split state durations. These were specified with  
105 random parameters within the bounds [1,5]. These bounds were decided upon after visual inspection  
106 of many Monte Carlo simulated buildup functions. We draw the first sample from the distribution  
107 corresponding to the grouped state, the second from that corresponding to the split state, and continue  
108 drawing samples from each distribution in alternation until the sum of all the durations exceeds the  
109 length of a trial. These trial durations are converted into discretized timecourses by assigning a value  
110 of 0 to time intervals during which the state corresponds to a grouped percept, and assigning a value  
111 of 1 to the time intervals for which the percept state was split. In Monte Carlo simulations, we  
112 produce an arbitrarily large (1000 trials) number of such timecourses, then take the average at each

113 time point.

114 We have also derived an analytical solution to this process using a population density approach  
115 similar to that used in Stinchcombe et al. (2012) to model stochastic gene expression. There are a  
116 number of advantages to characterizing the buildup function in this way. First, with an analytical  
117 solution relating the distributions of durations for grouped and split percepts to the buildup function,  
118 it is theoretically possible to interconvert between buildup functions and the statistics of the  
119 dominance durations for each percept. We have developed this solution into a statistical switching  
120 model to reconstruct the buildup function from four parameters- the parameters for the gamma  
121 densities for grouped and split percept durations. This theoretical solution coincides with the Monte  
122 Carlo simulation results (see Figure 2b). This is convenient, as the analytical solution is  
123 computationally less expensive than iterative Monte Carlo simulations, and the solution is exact.

124 We wanted to test whether it was possible to recover the parameters for the long term statistics of  
125 dominance durations from the buildup function. To estimate the gamma parameters from Monte  
126 Carlo generated buildup functions, we used the analytical solution (below) and searched for the 4  
127 parameters that minimized the squared error between the analytical and the Monte Carlo generated  
128 buildup function. We also tested a constrained model that assumes that the duration distributions for  
129 grouped and split percepts are matched. All simulations were implemented in MATLAB. Maximum  
130 likelihood estimation was carried out using the gamfit function from the stats toolbox.

### 131 2.1. Solving analytically for the alternating renewal process

132 In the alternating renewal process there are 2 random variables,  $S(t)$  and  $Z(t)$ .  $S(t)$  is the random  
133 elapsed time since last switching into the current state, evaluated at time  $t$ .  $Z(t)$  is a dichotomous  
134 random variable, where  $Z(t)$  in  $\{0, 1\}$  codes for the percept, grouped or split. For sake of

135 convenience, we introduce 2 probability mass functions:

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

136 and

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

137

138 where  $s$  is the elapsed time since entering state  $i$  and  $h_{T_i}(s)$  is the hazard function, the probability per

139 unit time of exiting the current state at time  $t$ . This is characterized by  $h_{T_i}(s) = \frac{(f_{T_i})}{\hat{f}_{T_i}}$ , the ratio of the

140 density function of durations  $T_i$  for state  $i$  and its complementary cumulative distribution function.

141

142 The value of  $S(t)$  is reset to 0 whenever an alternation between states occurs. The initial flux of

143 probability (a source) at  $s = 0$  is determined by the probability of switches out of the previous state,

144 leading to the following boundary conditions:

145

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

146

147

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

148

149 The probability that  $Z(t) = 1$ ,  $p_1(t)$ , is the marginal probability mass function evaluated at  $z = 1$ . It

150 is obtained by integrating  $f_1(s, t)$  over all s; and similarly for  $Z(t) = 0$ . We used the following initial  
 151 conditions, corresponding to  $\Pr\{Z(t = 0) = 1\} = 1$ , and  $\Pr\{Z(t = 0) = 0\} = 0$ . In some  
 152 experimental contexts, it has been observed that the first percept duration for an ambiguous stimulus  
 153 is longer than subsequent durations (see Discussion). In order to accommodate for this possibility, we  
 154 first solve for the case of beginning in state 1:

155

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

156

157 For the sake of simplifying notation, we define  $p_{1|1}(t) = \Pr\{Z(t) = 1 | Z(t = 0) = 1\}$ .

158

159 Using these conditions yields the following solution:

160

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

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

162

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

166

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

167

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

169

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

170

171 Using the simplifying assumption that  $f_{T_0^0}(t) = f_{T_0}(t)$ , that is, that the initial percept duration is

172 from the same density function as all other  $T_0$ , we find:

173

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

174 At  $\omega = 0$ ,  $\hat{f}(\omega) = \mu(T_1)/(\mu(T_1) + \mu(T_0))$ . From here, the function in the time domain is obtained

175 by taking the inverse Fourier transform and finding the integral from 0 to  $t$ .

176

## 177 2.2. Competition model simulations

178 We wanted to use the competition model as a test-bed for the theory of the alternating renewal  
 179 process for different dynamical regimes of perceptual alternation- in particular, for noise-driven  
 180 switches, for which correlation between successive dominance durations is low, and for adaptation-  
 181 driven switching, for which correlation is high. We chose to modify existing observer models for  
 182 perceptual bistability to produce buildup functions to see if we could relate these to the underlying  
 183 dominance durations using renewal theory. Previous investigations (Wilson and Cowan (1972);  
 184 Wilson (2003); Laing and Chow (2002); Shpiro et al. (2009); Pastukhov et al. (2013)) have used  
 185 population firing rate models with competition architecture to model perceptual bistability. In these  
 186 pseudoneuronal mutual inhibition models, there are separate populations whose firing rates represent  
 187 the perceptual strength of each interpretation of the stimulus. They make inhibitory connections onto  
 188 one another, so the population with the highest firing rate typically dominates the other (Figure 5a).

189 These models were originally developed to describe binocular rivalry, but have also been used to  
190 account for the psychophysical results of experiments with ambiguous grouping—namely, moving  
191 plaids with coherent/transparent motion (Shapiro et al. (2009); Laing and Chow (2002); Pastukhov et  
192 al. (2013)) and triplets with streaming/integration/segregation (Mill et al. (2013)).

193

194 In competition models, the relative firing rates of the two populations are taken to produce the  
195 simulated observer's perceptual reports. The population with the higher firing rate corresponds to the  
196 dominant percept. Because the two populations mutually inhibit each other, in most cases only one  
197 population is active at any given time. In addition, each population undergoes adaptation in response  
198 to its own firing rate. The alternation of dominance epochs between the two populations can be  
199 driven by two mechanisms. If adaptation is strong enough, then the activity of the dominant  
200 population will decay over time, while the suppressed population recovers from any prior adaptation.  
201 This leads to periodic alternations between dominance states with oscillation dynamics. However, if  
202 adaptation is weak, the system will display attractor dynamics, in which alternations are driven by  
203 noise in the externally applied inputs. The brain appears to be a very noisy system, with random  
204 fluctuations occurring at multiple scales such as vesicular release and spiking variability.

205

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

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

208

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

216

217 The simulation was carried out in nondimensionalized time, with the convention that one unit of time  
 218 corresponds to 10 msec. Time constants given in simulation time units were  $\tau_a = 200$ ,  $\tau_n = 10$ . The  
 219 following parameter values are used:  $k = 0.1$ ,  $\theta = 0$ ,  $\beta = 1$ . For attractor dynamics, we set the value of  
 220 the external inputs to populations  $I_1$  and  $I_2$  to 0.6, the adaptation gain  $\gamma$  to 0.1, and the noise strength  
 221  $\sigma$  to .12. For oscillation dynamics, we set the value of the external inputs to populations  $I_1$  and  $I_2$  to  
 222 0.6, the adaptation gain  $\gamma$  to 0.3, and the noise strength  $\sigma$  to .09. The value of  $\sigma$  was scaled in relation  
 223 to the integration time step by  $1/\sqrt{dt}$  to keep specified variance per unit time. Simulations were  
 224 implemented in MATLAB using forward Euler integration with a time step of 0.1 (1 msec real time).

225

226 We chose initial conditions that ensured that the grouped percept was always dominant at the  
227 beginning of the trial, as our hypothesis that alternations could produce buildup relies on this  
228 assumption. We did this in a very simple manner (see Figure X), by setting the initial condition on  
229 the population representing the grouped percept to half its maximum value. For each combination of  
230 parameter values, we simulated 500 trials of length 20 s with initial conditions  $u_2(0)$ ,  $a_1(0)$ ,  $a_2(0)$ ,  
231  $n_1(0)$ ,  $n_2(0) = 0$  and  $u_1(0) = 0.5$ ; thus, at the beginning of each simulated trial, the first  
232 population to become dominant was always that corresponding to the grouped percept. Simulated  
233 experimental buildup curves were constructed by computing the average for each time point across  
234 trials of the binary timecourse  $u_2 > u_1$ .

235

236 We obtained dominance durations by finding time points of the zero crossings of the differences of  
237 the firing rate timecourses. To test the application of the alternating renewal process model, we  
238 viewed dominance durations of each state from the short simulated trials as samples from underlying  
239 gamma distributions. Because our competition model simulations generated trials that were only 20  
240 seconds long, a large proportion of these durations were truncated by the end of the trial. We  
241 estimated gamma parameters  $k$  and  $\theta$  that maximized the likelihood of the complete as well as the  
242 right-censored dominance durations for each model perceptual state. Using the samples of dominance  
243 durations obtained for each population (over 1000 durations for each population with each parameter  
244 set), we fitted gamma densities using maximum likelihood estimation. We compared the simulated  
245 empirical buildup functions with those predicted under our statistical model using these fitted gamma  
246 parameters by computing  $R^2$ , the coefficient of determination.

247 **3. Results**

248 **3.1. Monte Carlo simulated and analytically computed buildup functions converge, but  
249 duration distributions are not well constrained by the buildup function**

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

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

270 However, for the special case when the both perceptual states have identical duration distributions,  
271 the parameter estimation for the gamma density functions from the buildup function is much better.  
272 This circumstance occurs in competition model simulations when the inputs to the populations  
273 representing each percept are matched, e.g., when the stimulus is perfectly ambiguous. We generated  
274 buildup functions using Monte Carlo simulations from two identical gamma densities, and found the  
275 single pair of gamma parameters that minimized squared error between this and theoretical buildup  
276 function (Figure 4). For 1000 such simulations, 63% of the recovered parameters were  
277 indistinguishable from the sample empirical distribution by Kolmogorov-Smirnov tests, and in  
278 general the fits were much closer, with a mean KS distance of .04. This method of estimation may  
279 prove useful for providing at least a rough estimate of the duration distributions underlying steady  
280 state switching dynamics.

281 **3.2. Competition model simulations produce buildup functions consistent with an  
282 alternating renewal process, even when trial timecourses violate assumptions**

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

293 The difference between oscillator and attractor dynamics in these competition models is most simply  
294 understood by observing how the system would behave without noise (Shapiro et al. (2009); Moreno-  
295 Bote et al. (2007)). For oscillation dynamics, adaptation would cause the dominant population to  
296 reduce its activity over time, reducing the inhibition on the suppressed population, allowing it to  
297 become active. In a noiseless system, stable fixed points in the system appear and disappear over  
298 time, and alternations will occur deterministically with a constant period. Noise in such a system will  
299 affect the distribution of dominance durations for each state, but is not required for switching.  
300 Conversely, attractor dynamics occurs when a system has multiple stable states at the same time. In  
301 the absence of noise, the initial conditions determine which state becomes active, and the system  
302 behaves in a winner-take-all fashion. That is, the population that becomes dominant first is  
303 permanently active, and the other population is permanently suppressed. However, injecting noise  
304 into such a system can cause switches from one stable state into another. In this case, the switching  
305 between perceptual dominance states is caused by the noise itself.

306 When the switches between perceptual states are driven by noise, as under attractor dynamics,  
307 correlations between successive dominance durations are low ( $r \approx .12$ ). An example trial timecourse  
308 is shown in Figure 5b, top. By averaging over many trials the dominance state  $u_2 > u_1$ , we obtain a  
309 simulated empirical buildup function. We fitted gamma parameters to the dominance durations, and  
310 used these parameters to generate analytical buildup functions using the alternating renewal process  
311 model (Figure 5b, bottom). The prediction of buildup function for an alternating renewal process  
312 with the underlying duration distributions with those fitted gamma parameters very strongly fits ( $R^2$   
313 = 98%) the buildup function obtained empirically by averaging over many trials.

314 **3.2.1. Oscillation dynamics produces buildup functions that dramatically differ from those**

**315 previously reported in psychophysical experiments**

316 Previous work from our lab has shown that oscillation dynamics are inconsistent with a number of  
317 statistical features of the dominance durations reported in psychophysical experiments (Shapiro et al.  
318 (2009)). The mean and circular variance of dominance durations under these dynamics do not fall  
319 within the range of those observed for perceptual reports of ambiguous visual displays. Furthermore,  
320 when adaptation drives alternations in the dominance of population activity, we observe moderate  
321 and significant correlations between successive percepts. Data from the psychophysical literature  
322 suggests that the durations of subsequent percepts are only weakly correlated, if at all (Pressnitzer  
323 and Hupé (2006)).

324 We wanted to examine buildup under each of these dynamical regimes in order to determine whether  
325 we could find correspondence between the buildup functions produced by competition models and  
326 those reported in the psychophysical literature. Previously reported psychophysical data indicate that  
327 the buildup function is monotonic. To our knowledge, no psychophysical experiments have shown a  
328 buildup function timecourse with a damped oscillatory approach to steady state. Buildup functions  
329 produced under oscillation dynamics in our competition model (Figure 6), however, display damped  
330 oscillations reflecting the underlying periodicity of the mechanism of alternation from the oscillator  
331 regime. As previously reported Shapiro et al. (2009), these buildup functions are derived from  
332 perceptual timecourses for which there are significant correlations between successive percept  
333 durations, such that the present perceptual state depends on the cumulative history of previous  
334 percepts. Although the correlation coefficient between durations of subsequent percepts was  
335 significant ( $r = 0.28$ ), the fit to the buildup function by finding the parameters of density functions  
336 for long term percept durations was strong ( $R^2 = 93\%$ ). Despite ignoring history dependence, the

337 theory linking buildup to long-term dynamics gives accurate predictions.

338 **4. Discussion**

339 **4.1. What if the first percept is longer?**

340 One issue we have not addressed so far in our presentation of the alternating renewal process model  
341 is inertia (Hupé and Pressnitzer (2012)). For ambiguous displays, the time until the first perceptual  
342 switch is typically much longer than subsequent durations of the same percept. For stimuli with  
343 ambiguous grouping, the distribution of initial grouped percept durations is different from other  
344 grouped percepts. In some experimental data collected with short trials, this might not be especially  
345 concerning— most trials contain one or fewer switches, i. e., from the integrated to the segregated  
346 percept. With these data, the distribution of initial switch times would be sufficient to describe a  
347 renewal process accounting for buildup. For data collected from longer trials with many alternations,  
348 however, it might be desirable to distinguish between initial and subsequent grouped percept  
349 durations. Our theoretical model is capable of computing the buildup function from both steady state  
350 and initial percept distributions; however, this would introduce a third duration distribution, and  
351 increase the number of parameters to 6. For simplicity's sake, we have only shown the 4-parameter  
352 model, which assumes that the initial percept duration is drawn from the same distribution as other  
353 grouped percept durations.

354 To adequately explain these perceptual dynamics with a physiological model, there should be some  
355 description of the sensory coding mechanisms that underlie the formation of perceptual organization.  
356 The specific mechanisms for switching in human stream segregation may be complex; (Kondo and  
357 Kashino (2009)) find that feedforward and feedback processes in a thalamocortical loop might be  
358 differentially engaged for switches into and out of the perceptual organization that is strongest. The

359 renewal process model is agnostic to the specific mechanism by which states are found and  
360 alternations occur; we have used existing competition models for the sake of illustration and as a  
361 computational test-bed. Similar competition-like processes have been used to explain the alternations  
362 observed in ambiguous motion Pastukhov et al. (2013) and stream segregation (Mill et al. (2013)  
363 experiments). A better understanding of the characteristics of the neural populations on the encoding  
364 side of perceptual organization could enable us to more accurately model the psychophysical data.

365 Our theoretical solution can be modified to account for experimental data in which the initial percept  
366 duration distribution is different from the steady state. However, there are circumstances in which  
367 inertia is fairly trivial, such as when buildup resets after a switch in attention (Denham et al. (2010)).  
368 Stationary distributions might be appropriate for such circumstances. We can take a more abstract  
369 view and consider a steady-state buildup function constructed from averaging over timepoints  
370 aligned by switches into the grouped percept.

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

380 **4.2. Do correlations between successive perceptual state durations matter for describing  
381 buildup functions?**

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

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

405 split perceptual organization may therefore be seen as complementary with the habituation-based  
406 explanation for the buildup function.

407 What is still missing from these theories, however, is the mechanism by which the perceptual state  
408 switches back and undergoes alternations; how do we account for switches out of the split percept?  
409 Our statistical model is agnostic to the mechanism of switching, but it does use information about  
410 alternations to predict perceptual dynamics. This is a novel insight linking transient dynamics to any  
411 underlying steady state process generating alternations, and produces surprisingly good predictions  
412 with minimal assumptions.

413 **5. Acknowledgement**

414 This is a short text to acknowledge the contributions of specific colleagues, institutions, or agencies  
415 that aided the efforts of the authors. A statement about the principal source of funding should be  
416 inserted if appropriate, including grant numbers if appropriate.

417 **6. References<sup>1</sup>**

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<sup>1</sup> Provide the doi when available, and ALL complete author names.

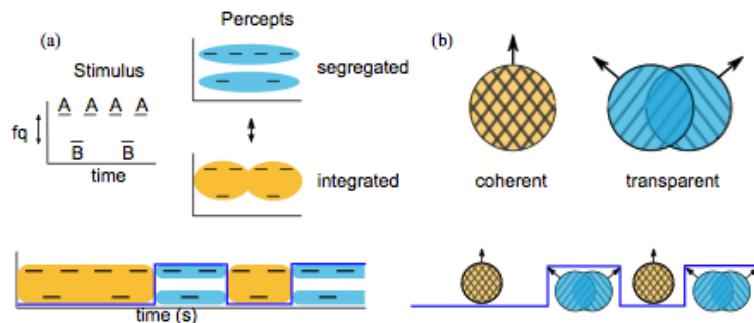
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## 7. Figure legends

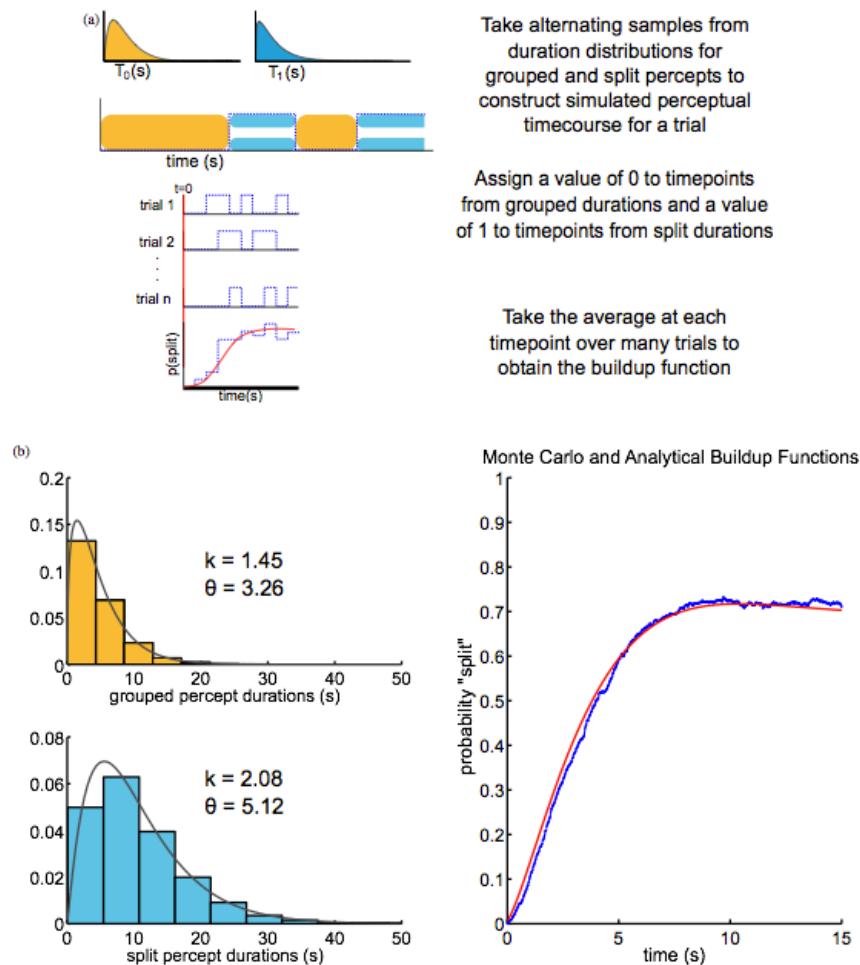


430

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

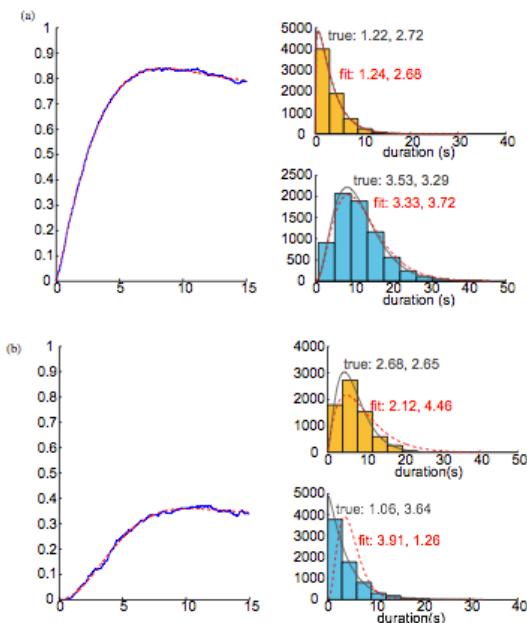
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438

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



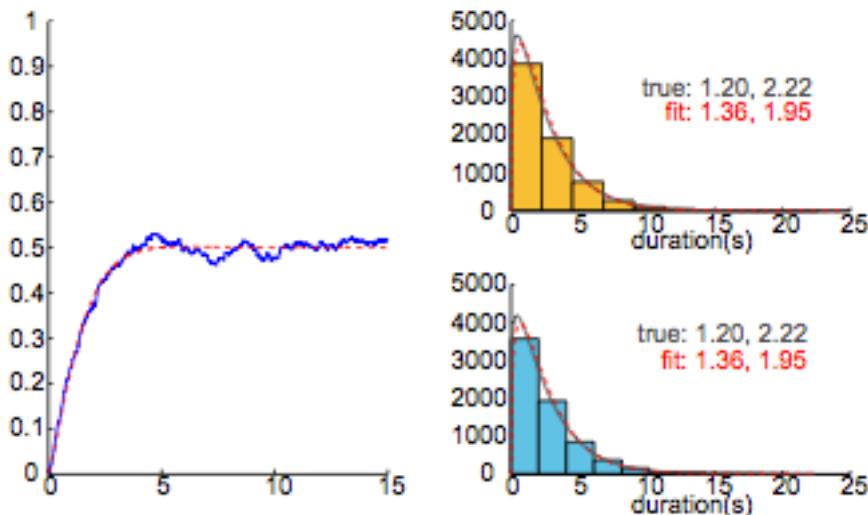
446

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

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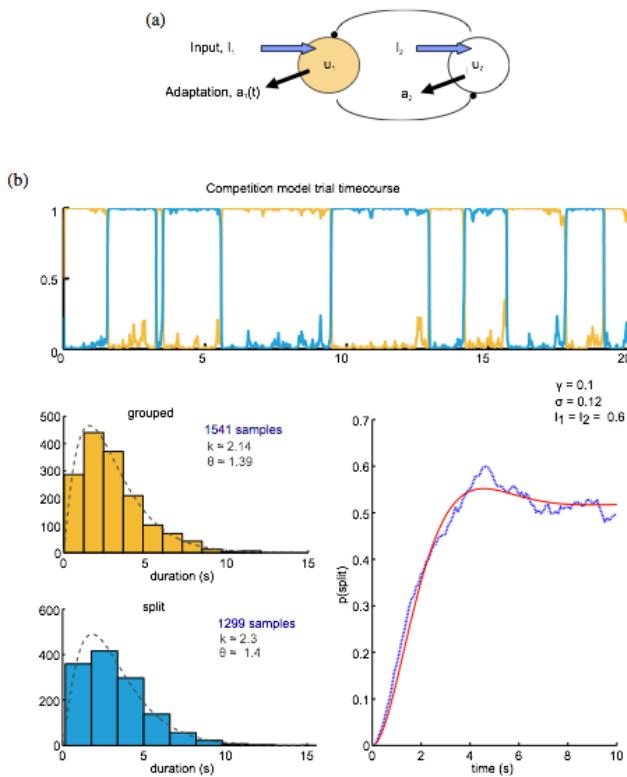
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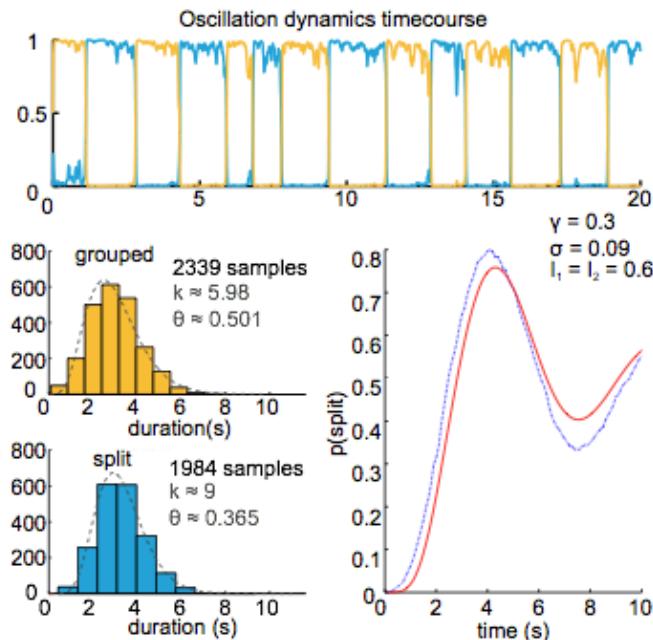
458

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



463

464 **Figure 5:** (a) Mutual inhibition population firing rate model producing buildup. We choose initial  
 465 conditions to ensure that the population representing the grouped percept,  $u_1$ , is always dominant at  
 466 the beginning of a given trial timecourse. (b) Competition model simulation results for parameters  
 467 that produce attractor dynamics with noise-driven switching. Top, population activity timecourse for  
 468 one 20-second trial. We simulated 500 trials to produce the buildup function, lower right (blue).  
 469 Histograms of the dominance durations, with maximum likelihood estimated gamma density  
 470 parameters and the associated density functions (gray), are shown in the lower left. These parameters  
 471 allow us to compute analytically the resulting buildup function for an alternating renewal process  
 472 (red). The buildup function looks similar to those reported in the psychophysical literature, and the  
 473 statistical model's prediction is good ( $R^2 = 98\%$ ).



474

475 **Figure 6:** Competition model simulation results for parameters that produce oscillation dynamics  
 476 with adaptation-driven switching. Top, population activity timecourse for one 20-second trial. The  
 477 dominance durations are much more regularly timed than those produced under attractor dynamics,  
 478 reflecting the clock-like periodicity of the underlying oscillator. These oscillations are dramatically  
 479 present in the average over 500 simulated trials, lower right (blue). To our knowledge, no such  
 480 buildup functions have been observed psychophysically. The maximum likelihood estimated gamma  
 481 density parameters are shown in the lower left (gray), and the analytically computed buildup function  
 482 for an alternating renewal process with those parameters is shown in the lower right (red). The fit  
 483 between the analytical solution and the trial average is still quite good ( $R^2 = 93\%$ ).

484

485

486 **8. Supplementary Material**

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

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

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