



## Relating accumulator model parameters and neural dynamics



Braden A. Purcell<sup>a,\*</sup>, Thomas J. Palmeri<sup>b</sup>

<sup>a</sup> Center for Neural Science, New York University, New York, NY 10003, United States

<sup>b</sup> Vanderbilt University, United States

### HIGHLIGHTS

- Neural analyses are used to quantify changes in accumulator model dynamics.
- Accumulator model dynamics distinguish models that behavior alone cannot.
- However, analysis of dynamics alone cannot pinpoint underlying model parameters.
- Joint consideration of behavior and neural dynamics provides maximal constraint.

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### ABSTRACT

Accumulator models explain decision-making as an accumulation of evidence to a response threshold. Specific model parameters are associated with specific model mechanisms, such as the time when accumulation begins, the average rate of evidence accumulation, and the threshold. These mechanisms determine both the within-trial dynamics of evidence accumulation and the predicted behavior. Cognitive modelers usually infer what mechanisms vary during decision-making by seeing what parameters vary when a model is fitted to observed behavior. The recent identification of neural activity with evidence accumulation suggests that it may be possible to directly infer what mechanisms vary from an analysis of how neural dynamics vary. However, evidence accumulation is often noisy, and noise complicates the relationship between accumulator dynamics and the underlying mechanisms leading to those dynamics. To understand what kinds of inferences can be made about decision-making mechanisms based on measures of neural dynamics, we measured simulated accumulator model dynamics while systematically varying model parameters. In some cases, decision-making mechanisms can be directly inferred from dynamics, allowing us to distinguish between models that make identical behavioral predictions. In other cases, however, different parameterized mechanisms produce surprisingly similar dynamics, limiting the inferences that can be made based on measuring dynamics alone. Analyzing neural dynamics can provide a powerful tool to resolve model mimicry at the behavioral level, but we caution against drawing inferences based solely on neural analyses. Instead, simultaneous modeling of behavior and neural dynamics provides the most powerful approach to understand decision-making and likely other aspects of cognition and perception.

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Cognitive modeling allows us to infer the mechanisms underlying perception, action, and cognition based on observed behavior (Busemeyer & Diederich, 2009; Farrell & Lewandowsky, 2010; Townsend & Ashby, 1983). In the domain of decision-making, *accumulator models* (also called *sequential-sampling models*) provide the most complete account of behavior for many different types of decisions (Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; Brown & Heathcote, 2005, 2008; Laming, 1968; Link, 1992; Link & Heath,

1975; Nosofsky & Palmeri, 1997; Palmer, Huk, & Shadlen, 2005; Ratcliff & McKoon, 2008; Ratcliff & Smith, 2004; Reddi & Carpenter, 2000; Shadlen, Hanks, Churchland, Kiani, & Yang, 2006; Smith & Vickers, 1988; Usher & McClelland, 2001; Vickers, 1979). These models assume that evidence for a particular response is integrated over time by one or more accumulators. A response is selected when evidence reaches a response threshold. Variability in the time it takes for accumulated evidence to reach threshold accounts for variability in choice probabilities and response times observed in a broad range of decision-making tasks.

Particular accumulator model parameters represent distinct decision-making mechanisms (Fig. 1). An *encoding time* ( $t_e$ )

\* Corresponding author.

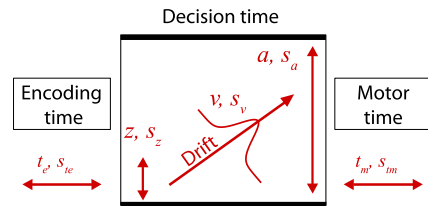
E-mail address: [braden@nyu.edu](mailto:braden@nyu.edu) (B.A. Purcell).

parameter defines the time for sensory and perceptual processing, a *drift rate* parameter ( $v$ ) defines the mean rate of evidence accumulation, a *starting point* parameter ( $z$ ) determines the initial state of an accumulator, a *threshold* parameter ( $a$ ) defines the level of evidence that must be reached before a response is initiated, and a *motor response time* ( $t_m$ ) parameter defines the time to execute a response (Fig. 1(A)). By identifying parameter values that maximize the match between observed and predicted behavior (e.g. Vandekerckhove & Tuerlinckx, 2007), the models can reveal the mechanisms underlying variation in decision-making behavior across different experimental conditions. For example, manipulations of speed versus accuracy instructions affect the response threshold (Brown & Heathcote, 2008; Wagenmakers, Ratcliff, Gomez, & McKoon, 2008), manipulations of experience (Nosofsky & Palmeri, 1997; Palmeri, 1997; Petrov, Van Horn, & Ratcliff, 2011; Ratcliff, Thapar, & McKoon, 2006) or stimulus strength (Palmeri et al., 2005; Ratcliff & McKoon, 2008; Ratcliff & Rouder, 1998) affect drift rate, and manipulation of dynamic stimulus noise prolong encoding time (Ratcliff & Smith, 2010). In addition, many accumulator models assume that some of these mechanisms can vary over trials to explain within-condition variability in behavior, with additional parameters defining the degree of variability in other parameters.

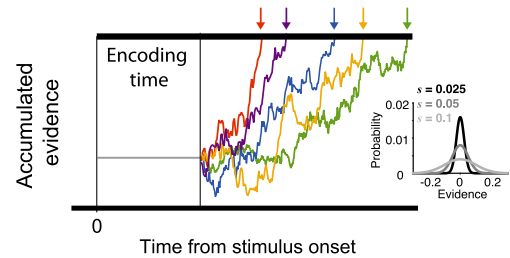
Recent neurophysiological and neuroimaging studies have identified potential linking propositions (Schall, 2004; Teller, 1984) between accumulator models and measures of brain activity (Forstmann, Ratcliff, & Wagenmakers, 2015; Forstmann, Wagenmakers, Eichele, Brown, & Serences, 2011; Gold & Shadlen, 2007; Palmeri, Schall, & Logan, 2014; Shadlen & Kiani, 2013; Smith & Ratcliff, 2004). Different approaches have established different kinds of connections between models and neural measures (Turner, Forstmann, Love, Palmeri, & Van Maanen, 2017). One approach has been to fit a model to behavior, and use the fitted parameters as a tool for interpreting or identifying neural signals. Correlating model parameters and neural signals across subjects and conditions can provide insight into what brain regions might be involved in determining the model threshold, drift rate, and non-decision time (Forstmann et al., 2008; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; van Maanen et al., 2011; White, Mumford, & Poldrack, 2012). Another approach has been to jointly model behavioral data and neural responses together, significantly constraining parameter estimates (Cassey, Gaunt, Steyvers, & Brown, 2016; Turner, van Maanen, & Forstmann, 2015).

Another line of work suggests that the firing rates of certain neural populations directly represent the evidence accumulation process proposed in the accumulator model framework. In these studies, animals are trained to perform perceptual decision-making tasks and neural activity is recorded from one or more intracranial electrodes simultaneously while animals perform the task. Neural responses can then be analyzed aligned to the timing of task events (e.g., stimulus onset) or the behavior of the animal (e.g., response initiation). Specifically, the firing rates of neurons within a distributed network of areas including prefrontal cortex (Ding & Gold, 2012; Hanes & Schall, 1996; Heitz & Schall, 2012; Kiani, Cueva, Reppas, & Newsome, 2014; Kim & Shadlen, 1999; Mante, Sussillo, Shenoy, & Newsome, 2013; Purcell et al., 2010; Purcell, Schall, Logan, & Palmeri, 2012), superior colliculus (Horwitz & Newsome, 1999; Ratcliff, Cherian, & Segraves, 2003; Ratcliff, Hasegawa, Hasegawa, Smith, & Segraves, 2007), posterior parietal cortex (Churchland, Kiani, & Shadlen, 2008; de Lafuente, Jazayeri, & Shadlen, 2015; Mazurek, Roitman, Ditterich, & Shadlen, 2003; Roitman & Shadlen, 2002), premotor cortex (Cisek, 2006; Thura & Cisek, 2014; Thura, Cos, & Cisek, 2014), and basal ganglia (Ding & Gold, 2010) exhibit dynamics consistent with accumulation of perceptual evidence. Following the onset of a stimulus, the firing rates of these neurons gradually rise over

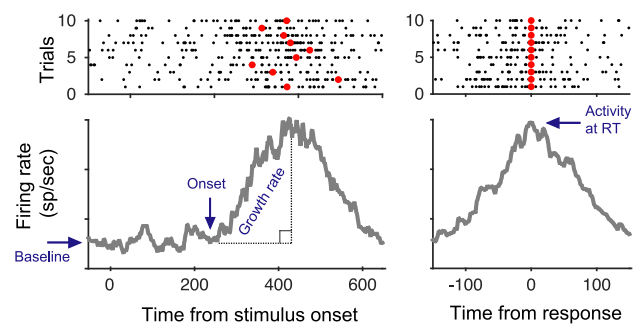
### A Accumulator model parameters



### B Example model dynamics



### C Example neural dynamics



**Fig. 1.** Expected relationships between accumulator model parameters, model dynamics, and neural dynamics. **A:** Illustration of accumulator model parameters. Four primary parameters determine the decision-making mechanisms: *encoding time* ( $t_e$ ) defines the time for perceptual processing preceding evidence accumulation, *drift rate* ( $v$ ) defines the mean rate of accumulation, *starting point* ( $z$ ) determines the initial state, *threshold* ( $a$ ) defines the level of evidence that must be reached before a response is initiated, and *motor response time* ( $t_m$ ) defines the time to execute a response. Four corresponding stochastic parameters ( $s$  with subscript) define the across-trial variability for each parameter (see Section 1). In these simulations, motor time was always assumed to be zero. **B:** Example model dynamics for five simulated trials using identical parameters. During encoding time, the model activity is fixed at the starting point. Following encoding time, evidence is sampled from a distribution with mean  $v$  and standard deviation  $s$  (within-trial noise, inset) and accumulated over time. Response times (RTs, arrows) are the sum of encoding time, the time needed for accumulated evidence to reach threshold (i.e., decision time). Due to within-trial noise, even the same set of parameters produces variability in both RT and the evidence accumulation trajectory. **C:** Example simulated single-unit activity and measures of neural dynamics. Top panels show that neural activity on individual trials given by the spike discharge times (black dots) aligned on stimulus onset (left) or RT (right; red circles). Individual spike trains are highly noisy, but the average firing rate over trials reveals underlying structure in the dynamics (gray lines, bottom). Four measures of neural dynamics are commonly applied to make inferences about model parameters. The onset is hypothesized to correspond to the encoding time, the growth rate is hypothesized to correspond to the drift rate, the baseline is hypothesized to correspond to the starting point, and the activity at RT is hypothesized to correspond to the threshold. Dashed black lines illustrate the computation of growth rate based on the slope of the line connecting the activity at onset to activity at RT. Neural spike times were simulated according to a time inhomogeneous Poisson process with a rate parameter determined by simulated accumulator model dynamics.

time depending on the animal's upcoming choice. Consistent with expected accumulator model dynamics, the rate of rise depends on stimulus strength and RT. Importantly, activity converges to a fixed firing rate shortly before the response is initiated regardless of the stimulus and RT, consistent with a threshold mechanism for decision termination (Hanes & Schall, 1996). The

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