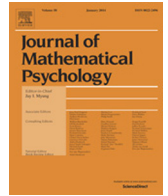




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A drift–diffusion model of interval timing in the peak procedure

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HIGHLIGHTS

- A review of individual trial analyses in the peak procedure is presented.
- The Time-adaptive Drift–diffusion Model is shown to be able to explain the data.
- TDDM is shown to be equivalent to Scalar Expectancy Theory under the peak procedure.
- DDMs might provide a comprehensive theory of decision making, choice and timing.

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ABSTRACT

Drift–diffusion models (DDMs) are a popular framework for explaining response times in decision-making tasks. Recently, the DDM architecture has been used to model interval timing. The Time-adaptive DDM (TDDM) is a physiologically plausible mechanism that adapts in real-time to different time intervals while preserving timescale invariance. One key open question is how the TDDM could deal with situations where reward is omitted, as in the peak procedure—a benchmark in the timing literature. When reward is omitted, there is a consistent pattern of correlations between the times at which animals start and stop responding. Here we develop a formulation of the TDDM's stationary properties that allows for the derivation of such correlations analytically. Using this simplified formulation we show that a TDDM with two thresholds – one to mark the start of responding and another the stop – can reproduce the same pattern of correlations observed in the data, as long as the start threshold is allowed to be noisy. We confirm this by running simulations with the standard TDDM formulation and show that the simplified formulation approximates well the full model under steady-state conditions. Moreover, we show that this simplified version of the TDDM is formally equivalent to Scalar Expectancy Theory (SET) under stationary behaviours, the most prominent theory of interval timing. This equivalence establishes the TDDM as a more complete drift–diffusion based theory with SET as a special case under steady-state conditions.

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1. Introduction

Learning the time between important events is a fundamental feature of cognition. Humans and other animals can readily learn the timing of upcoming rewards and adapt their behaviour accordingly (Buhusi & Meck, 2005; Grondin, 2010). A range of psychological and computational theories have been proposed for interval timing (Gibbon, 1977; Grossberg & Schmajuk, 1989; Killeen & Fetterman, 1988; Ludvig, Sutton, & Kehoe, 2008; Machado, Malheiro, & Erilagen, 2009; Simen, Rivest, Ludvig, Balci,

& Killeen, 2013; Staddon & Higa, 1999) which succeed at capturing the broad outlines of timing behaviour, but they often flounder when dealing with the statistics of the micro-structure of real-time responding.

Particularly vexing for timing models are the behavioural patterns when predictably-timed rewards are occasionally omitted, as in the peak procedure (Roberts, 1981). This peak procedure is likely the most popular interval timing task. Although major timing models such as Scalar Expectancy Theory (SET) (Gibbon, 1977), Behavioural Theory of Timing (BeT) (Killeen & Fetterman, 1988), Learning to Time (LeT) (Machado, 1997; Machado et al., 2009) and Multiple Time Scales (MTS) (Staddon & Higa, 1999) can reproduce the global averaged behaviour in this task, very few models have been able to account for the pattern of behaviour observed in individual trials. The notable exception is SET, which provides good

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quantitative fits to animal data (Church, Meck, & Gibbon, 1994) and remains the theory of choice for explaining static timing phenomena.

Recently, a series of studies have adapted the classic drift-diffusion model (DDM) used to explain the dynamics of real-time decision-making in behaviour and the brain (Gold & Shadlen, 2007; Ratcliff, 1978; Voss, Nagler, & Lerche, 2013) to interval timing (Luzardo, Ludvig, & Rivest, 2013; Rivest & Bengio, 0000; Simen, Balci, de Souza, Cohen, & Holmes, 2011a; Simen et al., 2013). The Time-adaptive DDM (TDDM) explains timing as the result of a noisy drift-diffusion process with an adaptive drift rate, which is adjusted based on the time interval observed. The TDDM has a plausible neural implementation, in that the formalism is also a mathematical approximation of the net effect of excitation and inhibition in the activity of a pool of neurons (Simen et al., 2011a). The model builds on earlier theories, such as SET, by adopting a different, more complete mathematical formulation that allows modelling the trial-by-trial dynamics of timing (i.e., the learning), while still explaining core properties of interval timing (such as timescale invariance). The general modular architecture (accumulator, memory storage and decision rules) is preserved, however, raising interesting questions as to the exact formal relationship between the TDDM and SET.

The TDDM has been successfully applied to some key features of interval timing. Most notably, it can account for the scalar property, a ubiquitous feature of timing data where the distribution of response times scales with the interval being timed. The model has also been shown to learn quickly and to reproduce the behaviour observed in fixed-interval schedules (Rivest & Bengio, 0000), the bisection procedure (Balci & Simen, 0000), and tasks where time intervals are changing either randomly (Simen et al., 2011a) or cyclically (Luzardo et al., 2013), but has been only cursorily applied to the aggregate data in the peak procedure thus far (Simen et al., 2013).

One of the main advantages of a mathematical model is the capacity to derive precise quantitative predictions from as few assumptions as possible. In this respect, the TDDM is particularly well placed among other timing models. As previously demonstrated (Simen et al., 2013), Weber's law, which in the context of interval timing manifests itself as a constant coefficient of variation (CV), follows from adjustments made to the parameters of the inverse Gaussian distribution predicted by the model. In contrast, SET's main theoretical component – a Poisson pacemaker – cannot by itself produce a constant CV. The usual solution is to add an assumption that the noise in the memory for the remembered intervals is so large as to overcome the noise in the pacemaker. This solves the problem but at the cost of adding an extra assumption and doing away with the Poisson pacemaker.

In this paper, we show that the TDDM can account for both the global averaged response curve in the peak procedure – and reproduce the statistics of behaviour in individual trials. We demonstrate this first analytically, through a new simplified formulation of TDDM's stationary properties, which we then show is equivalent to a constrained version of SET. The analytical results from the simplified model are then validated through simulations with the complete TDDM formulation.

These results extend the range of phenomena for which the TDDM can account and suggest that the Poisson pacemaker postulated by SET – but not actually used – may be substituted by the result of an opponent Poisson process (Simen et al., 2013). Furthermore, and in light of previous successes, these results suggest there might be a single comprehensive drift-diffusion-based theory of decision making and timing, which could cover both the steady-state properties as well as the learning dynamics.

The paper next reviews the studies that have examined the patterns of correlations in single-trial analyses of the peak

procedure. We then revisit the TDDM and develop a simplified stochastic model approximating TDDM's stationary properties. Given that formulation, the simplest possible extension of TDDM to support start and stop behaviours is analytically derived. This simplified formulation is shown to be equivalent to a constrained version of SET with two thresholds (Church et al., 1994), and shown to be a good approximation of the full TDDM through simulations. Finally, some predictions are made with the full TDDM about possible sequential effects in the peak procedure.

1.1. Peak Procedure

In the peak procedure subjects are first trained on a fixed-interval (FI) schedule where the first response after an interval has elapsed since the appearance of a stimulus produces a reward (see diagram on the left in Fig. 1). When behaviour on FI trials has stabilized, peak trials are then introduced. These peak trials are interspersed randomly between the normal FI trials, last 3 or 4 times longer, and are not rewarded. When peak trials are first introduced during training, animals start responding as usual before the FI time and then continue responding throughout the whole (long) interval. With sufficient experience with the peak trials, a different pattern emerges where responding eventually ceases or lowers in frequency soon after the expected reward time (Balci et al., 2009). This pattern of starts and stops that appears after sufficient training is the focus of our analysis here.

The panel on the right in Fig. 1 shows an example of how, when response rate is averaged over these peak trials even for a single individual, there is an apparent smooth, symmetrical rise and fall in responding around the time of reinforcement. When individual trials are analysed, however, a more abrupt shift in response rate is often observed. On many trials, animals start with a low response rate, switch to a high response rate, and then go back down again after the usual interval has elapsed and no reward has arrived (Church et al., 1994; Gallistel, King, & McDonald, 2004; Gibbon & Church, 1990). This three-state system (low-high-low) can be characterized by its two transition points: the start (switch from low to high) and stop (switch from high to low) times. In addition, the middle time and duration of the high-frequency bout can be calculated from the start and stop times.

A detailed analysis of these variables may shed light on the internal mechanisms of interval timing and provide constraints on current timing models. Table 1 collates the results from the major studies in the literature that have examined the statistics of these four variables. When possible we have separated the data by FI duration and, in only one case, also by reward magnitude. We did this because in a few cases the correlations were reported to be significantly different as a function of FI duration (Gallistel et al., 2004) and reward magnitude (Balci, Wiener, Cavdaroglu, & Branch Coslett, 2013), although this was not the norm. Of particular note are the coefficients of variation of each variable and their correlations. Note the strong similarity in the correlation patterns across 4 different species. The key results are as follows:

1. Positive correlation between start (S_1) and stop (S_2): $\rho(S_1, S_2) > 0$;
2. Negative correlation between start and duration (D): $\rho(S_1, D) < 0$;
3. Positive correlation between duration and middle (M): $\rho(D, M) > 0$;
4. Coefficient of variation (CV) for the start larger than for stop: $CV_{\text{start}} > CV_{\text{stop}}$.

The correlation results above mean that, in general, start times that occur early/late into the trial are usually followed by early/late stops. In contrast, the duration of the period of high frequency

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