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Approaching subjective interval timing with a non-Gaussian perspective

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Perceiving time intervals is an essential ability of many animals, whose psychophysical properties have yet to be fully understood. A common theoretical approach is to consider that internal representations of time intervals are reflected in probability distribution functions. Depending on the mechanism proposed for interval timing inverse Gaussian and log-normal probability distributions are candidate distributions to represent internal representations of time. In this article, we show that these two distributions approximate each other under the assumptions of mean accuracy and scalar timing when considering experimentally-relevant Weber fractions. Afterward, we show that both distributions may be used in the description of the temporal bisection task, predicting bisection times approximately at the geometric mean of reference time intervals for the experimental range of Weber fractions. Taken together these results suggest that the log-normal and the inverse Gaussian, when adapted to model subjective time intervals, are experimentally indistinguishable, and so are the models that use them as benchmarks.

1. Introduction

The way humans and other animals perceive time has been a popular matter of study for several decades. A central question regarding this matter is how time intervals are encoded or, in other words, how time intervals are internally represented.

One approach that has been taken in seminal papers was investigating whether the subjective time scale could be coded in a nonlinear (e.g. logarithmic or a power law of the physical time) fashion. In fact, both logarithmic and power law scales (the latter being associated with the scalar timing hypothesis) have been shown to be compatible with Weber's Law (Gibbon, 1981), also known as scalar property in the context of interval timing literature. This property states that the standard deviation and the mean of the distribution of a subject's timing responses covary linearly (Gibbon, 1977). Furthermore, several remarkable results from psychophysical experiments have indicated that logarithmic subjective magnitude scales better explain performance in abstract numerical and sensory tasks (Buzsáki & Draguhn, 2004; Dehaene, 2003; Dehaene, Izard, Spelke, & Pica, 2008; Nieder & Miller, 2003; Nover, Anderson, & DeAngelis, 2005).

The temporal bisection procedure is often used to investigate the psychophysics of interval timing. In this task, subjects are prompted with a forced binary choice protocol, to decide whether a newly presented time interval is closer to a shorter or a longer time reference. The stimulus duration for which subjects answer "short" or "long" in an equal number of trials is named bisection time. In a seminal bisection task article (Church & Deluty, 1977), rats showed bisection times at approximately the geometric mean of the reference intervals.

The log-normal distribution has been credited for describing a very general class of events associated with complex activity involving multiplicative noise (Limpert, Stahel, & Abbt, 2001). Psychometric functions of time have also been described through the use of log-normal distributions, to address the "log-timing" hypothesis (Gibbon, 1981). The assumption of normality in a putative logarithmic subjective time scale leads to the log-normal distribution since it is equivalent to a Gaussian distribution in a logarithmic scale (Fig. 1A). Gibbon has also shown (Gibbon, 1981) that bisection times should be equal to the geometric mean of reference intervals in the context of log-timing, if the likelihood ratio test from signal detection theory is used to compare short and long time intervals. This test consists in comparing the probabilities that a perceived time stimulus was generated by a short or a long time interval. The log-normal distribution also has the useful property of being the distribution of maximum entropy, if the logarithm of a random variable is constrained with fixed mean and variance (Park & Bera, 2009). An extensive review of the use of log-normal distributions in neuroscience has been published elsewhere (Buzsáki & Mizuseki, 2014).

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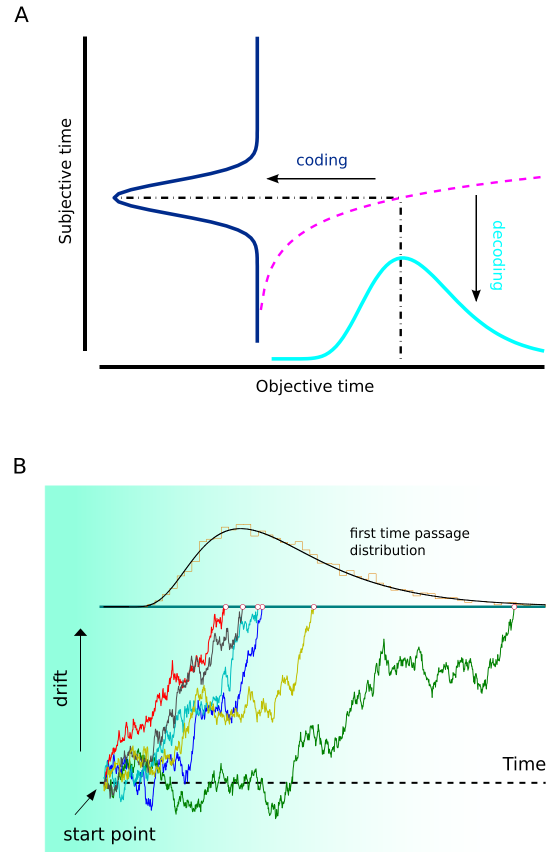

Fig. 1. Possible ways of generating Log-normal and inverse Gaussian in timing processes. (A) Rationale behind the observation of a log-normal distribution by the encoding process in a log scale. Encoding is represented as the transfer of a time interval from the objective time (horizontal axis) to the psychological time (vertical axis) through a logarithmic transformation. Even when the same interval is encoded repeatedly, the internal representation is noisy due internal noise of the encoding process, generating a Gaussian distribution of values in the subjective scale. Decoding is the inverse process, i.e. the transformation of values from a log-scale to a linear scale (exponential transformation). If one assumes that the objective time is encoded in a logarithmic scale (dashed purple curve), the Gaussian distribution is transformed to a log-normal distribution, shown by the response time distribution observed experimentally (cyan curve). (B) Drift–diffusion model leading to an inverse Gaussian distribution. Each line represents a decision variable subject to a drift–diffusion process. The red dots represent the instant in which a drift process crossed the threshold for the first time, called the first passage time. The histogram displays the counts of first passage times, and the continuous black line is the theoretical distribution of this random variable, the Inverse Gaussian distribution. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In a recently proposed drift–diffusion model of interval timing (Simen, Balci, Cohen, Holmes, et al., 2011), the inverse Gaussian distribution arises as the response time distribution, when we consider the moment the drift process crosses a response threshold for the first time (Fig. 1B). Additionally, this work showed that for small coefficients of variation, inverse Gaussian, gamma and Gaussian distributions approximate each other. Note that at least one other drift–diffusion based interval timing model has been proposed independently elsewhere (Rivest & Bengio). The drift–diffusion framework has also been successful in modeling temporal bisection, by use of a two-stage sequential diffusion process (Balcı & Simen, 2014). Inverse Gaussian distributions are also used to fit peak-interval data from other sets of experiments (Church, Lacourse, & Crystal, 1998; Church, Meck, & Gibbon, 1994). More recently, time-adaptive drift–diffusion models have been shown to explain behavior in peak-procedure tasks while being formally equivalent to the scalar expectation theory (SET) (Luzardo, Rivest, Alonso, & Ludvig, 2017).

Here, we show that log-normal and inverse-Gaussian probability distribution functions approximate each other and become experimentally indistinguishable for small Weber constants. Moreover, we could predict the experimental result that the bisection point is approximately equal to the geometric mean of the learned intervals, by using either distribution to model decision variables in a binary decision task.

This finding implies that a classic result in the bisection task can be equivalently obtained by using probability distribution functions that arise in diverse contexts within the theory of interval timing, namely drift–diffusion models and log-timing models. We expect that this finding will guide theoretical researchers in expanding and improving models for the encoding of time intervals.

2. Results

2.1. Log-normal and inverse Gaussian reparametrized distributions are numerically equivalent for small Weber constants

The bisection task (Church & Deluty, 1977) consists in training a subject to discriminate between a short (T_1) and a long (T_2) interval. After each stimulus is presented, the subject is required to produce one of two possible responses, e.g. pressing left or right lever. Each of these responses is associated with each reference interval so that only the correct response leads to reinforcement. By the end of the training phase, subjects are expected to reliably discriminate between short and long stimuli, producing the correct response after each presentation. In the testing phase, subjects are exposed to intervals whose durations are in between the short and long intervals. As in the training phase, they are also prompted with a binary forced decision. Subjects judge whether each intermediate interval is more similar to the short or the long reference interval, producing the response associated with them. The intermediate time interval stimulus at which subjects respond "short" or "long" with equal frequency – indicating maximal uncertainty – is named bisection time (Fig. 3).

Several interval-timing models directly or indirectly consider that perceived time intervals are better described by probability distribution functions (PDFs). Some of these models also create specific distinctions between the stages of perception, evaluation, and production of responses (Jazayeri & Shadlen, 2010), while others rely on a bottom-up strategy from single neurons to neuron clusters, in order to obtain an appropriate PDF model of timed responses (Matell & Meck, 2004; Simen et al., 2011).

Since we are interested in understanding the mathematical properties of PDFs that describe performance in a bisection task, we can use a simple model based on the signal detection theory framework, similarly to what has been done previously (Gibbon, 1981). In short, each reference time interval can be interpreted as a signal and represented internally through its associated probability distribution function. This allows for a straightforward interpretation of the bisection point as the point of greatest uncertainty between two time interval signals in a bisection task, as we will discuss further.

We define f_{X_i} as the distribution of the decision variable associated with time interval T_i, for $i = 1, 2$. The decision variable will be used as a criterion in the context of a bisection task in order to determine which interval has been presented to the subject in a given trial, "short", or "long". Our first objective is to draw conclusions based on two simple – yet fundamental – assumptions on f_{X_i}:

1. *Subjects time the target duration correctly on average (mean accuracy)*: The expected value of X_i is T_i.