

Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations

Graduate Studies

8-2020

Temporal Bisection Dynamics

Mahdi Shafiei

Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Psychology Commons](#)

Recommended Citation

Shafiei, Mahdi, "Temporal Bisection Dynamics" (2020). *All Graduate Theses and Dissertations*. 7828.
<https://digitalcommons.usu.edu/etd/7828>

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



TEMPORAL BISECTION DYNAMICS

by

Mahdi Shafiei

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Psychology

Approved:

Kerry Jordan, Ph.D.
Major Professor

Amy Odum, Ph.D.
Committee Member

Tyson Barrett, Ph.D.
Committee Member

Richard S. Inouye, Ph.D.
Vice Provost for Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2020

Copyright © Mahdi Shafiei 2020

All Rights Reserved

ABSTRACT

Temporal Bisection Dynamics

by

Mahdi Shafiei, Master of Science

Utah State University, 2020

Major Professor: Dr. Kerry Jordan
Department: Psychology

Temporal bisection is a long-used procedure to study the perception of time through a psychometric function; however, it is not fully clear how the parameters of this procedure collectively affect time perception. Moreover, it is not clear why experimental results are often different in human and animal temporal bisection literature. In this thesis, I propose a computational model that uses only the scalar property of timing and Bayesian learning to provide researchers with a platform that helps them understand the temporal bisection procedure in a dynamic “learning-decision” framework.

I specifically identify two problems in the way that the temporal bisection procedure is usually modeled and understood in the literature. First, a normal distribution is usually assumed for the perception of durations, while experimentally it is shown that the distribution of temporal perception is positively skewed. I demonstrate A) this assumption of normality for temporal perception evidently biases our understanding of time perception mechanisms, and B) how a positively skewed distribution could marry the computational and experimental literatures. Secondly, the importance of the learning process in a single trial of the testing phase is usually undermined in literature on the

temporal bisection procedure. In this thesis, I demonstrate how such a single-trial test phase learning process could affect our interpretation of temporal bisection results.

In sum, I demonstrate how computational modeling could affect our understanding of experimental results for the temporal bisection procedure. Thus, to further our understanding of cognitive and brain mechanisms, we should work to iteratively improve computational modeling to coevolve with experimental work.

(60 pages)

PUBLIC ABSTRACT

Temporal Bisection Dynamics

Mahdi Shafiei

Temporal bisection is a behavioral task used to study how we perceive time. However, it is not fully clear how time perception should be interpreted in different variations of this task. Moreover, it is not understood why the results of this task are often different for human and animal subjects. Understanding parameters of this task and making a connection between human and animal experiments may help researchers to understand how time is perceived in the brain and consequently disorders involving time perception.

In this thesis, I propose a computational model that A) provides researchers with a framework to study the parameters of the temporal bisection task to design better experiments and B) gives researchers an insight into potential underlying reasons for differences between human and animal time perception in this task. This model mimics subjects' learning and decision processes in making responses about the length of durations. By manipulating these processes, researchers should be able to verify how time perception is changed in different variations of the task. Additionally, this model helps researchers identify differences in learning and decision processes of human and animal subjects in temporal bisection, which could help explain more general differences in their time perception.

ACKNOWLEDGMENTS

I would like to thank Dr. Kerry Jordan and my committee members, Drs. Amy Odum, and Tyson Barrett for their time and assistance throughout the entire process. I would also thank Drs. Flann Nicholas and Breanna Studenka for their comments on the early drafts of this document.

I give special thanks to Ruth Campos for her encouragement, support, and patience as I worked my way from the initial proposal writing to this final document.

Mahdi Shafiei

CONTENTS

| | Page |
|--|------|
| ABSTRACT..... | iii |
| PUBLIC ABSTRACT | v |
| ACKNOWLEDGMENTS | vi |
| LIST OF TABLES | ix |
| LIST OF FIGURES | x |
| LIST OF EQUATIONS | xi |
| ACRONYMS..... | xii |
| INTRODUCTION | 1 |
| Importance..... | 3 |
| Aims | 4 |
| LITERATURE REVIEW | 5 |
| Range and Ratio of Anchor Durations | 5 |
| Spacing and Number of Test Durations | 7 |
| Type of Response Reinforcement | 8 |
| Leading Theories of Timing..... | 10 |
| Summary | 11 |
| METHODS | 12 |
| Normal Distribution for Temporal Perception | 12 |
| Positively Skewed and Scalar Distribution for Temporal Perception..... | 15 |
| Architecture of the Model | 20 |
| RESULTS | 27 |
| Learning vs No Learning..... | 27 |
| Logarithmic vs Linear Spacing | 33 |
| Number of Intermediate Durations | 36 |
| DISCUSSION | 39 |

| | |
|---|----|
| Limitations and Future Directions..... | 40 |
| Conclusion..... | 42 |
| DATA AVAILABILITY AND REPRODUCIBLE RESULTS..... | 44 |
| REFERENCES | 45 |

LIST OF TABLES

| Table | Page |
|--|------|
| 1 Parameters that are used in “Learning” vs “No Learning” conditions | 28 |
| 2 Durations and number of trials for linear and logarithmic spacing of test durations..... | 35 |
| 3 Durations and number of trials for three and seven test durations conditions..... | 37 |

LIST OF FIGURES

| Figure | Page |
|---|------|
| 1 Three normal distributions for temporal perception of a one second duration with different perceptual errors..... | 13 |
| 2 Assuming normal distributions for the perception of anchor durations locates the TIP in the HM of the anchor durations | 14 |
| 3 Cross-point of one second duration and 20 scaled normal distributions | 17 |
| 4 Positively skewed and scalar distributions for temporal perception of one second duration with different absolute errors..... | 18 |
| 5 Assuming the obtained positively skewed distribution for the perception of anchor durations locates the TIP in the AM of the anchor durations | 20 |
| 6 Diagram of a Bayesian model..... | 26 |
| 7 Center of the perceptual distribution for anchor durations over trials | 29 |
| 8 Psychometric function of responses without learning and with learning | 30 |
| 9 The relationship between positive and negative learning rates and the location of the TIP in a 3D plot | 31 |
| 10 The relationship between positive and negative learning rates and the location of the TIP in a 2D plot | 32 |
| 11 Psychometric function of responses using linear and logarithmic spacing of test durations | 36 |
| 12 Psychometric function of responses using 5 and 9 test durations..... | 38 |

LIST OF EQUATIONS

| Equation | Page |
|----------------------|------|
| 1 Equation 1 | 2 |
| 2 Equation 2 | 2 |
| 3 Equation 3 | 3 |
| 4 Equation 4 | 13 |
| 5 Equation 5 | 19 |
| 6 Equation 6 | 19 |
| 7 Equation 7 | 22 |
| 8 Equation 8 | 22 |
| 9 Equation 9 | 23 |
| 10 Equation 10 | 23 |
| 11 Equation 11 | 23 |
| 12 Equation 12 | 24 |
| 13 Equation 13 | 32 |
| 14 Equation 14 | 33 |

ACRONYMS

| | |
|-----|-----------------------------|
| TIP | Temporal Indifference Point |
| AM | Arithmetic Mean |
| GM | Geometric Mean |
| HM | Harmonic Mean |
| PD | Parkinson's disease |

CHAPTER I

INTRODUCTION

Temporal bisection is a long-used procedure to study the perception of time through a psychometric function (Cowles & Finan, 1941). In the standard format of this procedure, subjects learn to discriminate two durations, called anchor durations, as “Short” or “Long” and then are tested with novel durations between (often called intermediate) or even beyond (often called out-of-range) the anchor durations. Two sets of parameters could be defined in this task: intrinsic and extrinsic. Intrinsic parameters are those not specific to the experimental population or setting, while extrinsic parameters can be defined only by considering the experimental population or setting. Range of anchor durations, spacing of test durations, and reinforcement policy are examples of intrinsic parameters, while different treatments, stimulus modality, subject populations, priming, or experimental settings are considered examples of extrinsic parameters.

One of the most common measures in this procedure is the “Temporal Indifference Point,” (TIP) which is defined as an intermediate duration to which subjects are indifferent or classify as “Short” or “Long” with an equal probability. The location of TIP is a direct representation of subjective perception of time in subjects and is affected by both intrinsic and extrinsic parameters. For example, logarithmic as compared to linear spacing of test durations (intrinsic parameter) shifts the location of the TIP to the left (Wearden & Ferrara, 1995), and the TIP in Parkinson's disease (PD) patients as compared to control population (extrinsic parameter) shifts to the right (Mioni et al., 2018).

In recent decades, the relationship between the individual intrinsic parameters of this procedure and the location of the TIP has been widely investigated experimentally

(Reynolds & Catania, 1962; Stubbs, 1968, 1972; Church & Deluty, 1976; Platt & Davis, 1983; Raslear, 1975, 1983, 1985; Siegel, 1986; Wearden, 1991; Allan & Gibbon, 1991; Wearden & Ferrara, 1995, 1996; Wearden et al., 1997; Brown et al., 2005; Droit-Volet & Wearden, 2001; Droit-Volet et al., 2007; Akdogan & balci, 2016). However, it is unclear how these intrinsic parameters collectively affect the location of the TIP. This lack of knowledge has a root in the infeasibility of full factorial design with many factors. Moreover, there is a gap between the human and animal temporal bisection literature and theoretical explanations about the location of the TIP. The location of the TIP in human participants is consistently shown to be closer to the Arithmetic Mean (AM; see Equation 1) of anchor durations, while in animal subjects it is closer to the Geometric Mean (GM; see Equation 2) of anchor durations (Kopec & Brody, 2010); however, the reason for this discrepancy is not fully understood. On the other hand, Staddon and Higa (1999) argue that the scalar property of timing predicts the Harmonic Mean (HM; see Equation 3) of anchor durations as the location of the TIP regardless of subject species. In addition to the aforementioned problems, the effects of intrinsic parameters are not often consistent between individuals. For example, although there is a general consistency with regard to the influence of spacing of test durations on the location of TIP, there is considerable variability among subjects in the location of TIP, both within and between experiments (Allan, 2002).

$$AM(x, y) = \frac{x + y}{2} \quad (1)$$

$$GM(x, y) = \sqrt{x * y} \quad (2)$$

$$HM(x, y) = \frac{2 * (x * y)}{x + y} \quad (3)$$

Moreover, currently most of computational models for temporal bisection procedure assume a normal distribution for temporal perception of a duration (Gibbon, 1977); while, it has been experimentally shown that the distribution for temporal perception is positively skewed (Buhusi & Meck, 2005). In Methods section, the problems with assuming a normal distribution for temporal bisection will be discussed in more details.

Importance

Studies that are investigating the effect of extrinsic parameters in the temporal bisection procedure usually have a direct application to and impact on our understanding of time perception in different experimental conditions and populations. For example, the fact that the location of the TIP in PD patients shifts to the right as compared to the control population indicates that PD patients perceive durations shorter as compared to the normal population. In other words, since normal population's TIP is shorter than PD patients' TIP, PD patients are more likely to perceive the duration to which normal population are indifferent as short anchor duration than long anchor duration. On the other hand, studies that are investigating intrinsic parameters in this task usually do not provide any direct application or information for our understanding of temporal disorders. For example, the fact that we know if the long anchor duration is no more than four times the short anchor duration then the TIP will fall at the GM of the anchor durations (Platt & Davis, 1983), does not seem to be directly applicational. However, validity of statements involving extrinsic parameters depends on a solid understanding of intrinsic parameters' effects on the location of the TIP. Researchers need to study intrinsic parameters to design stronger

experiments that have appropriate controls for intrinsic parameters before making any statement about extrinsic parameters. For example, two studies that are identical in every aspect but spacing of test durations could yield totally different results about temporal perception of a specific population. Thus, any conclusion about time perception in extrinsically different experimental conditions in the temporal bisection procedure first requires a solid understanding of the intrinsic parameters' effect on the location of the TIP.

Additionally, the temporal bisection literature needs a theory that bridges the animal and human data and consequently gives researchers better insight about the mechanisms of time perception.

Aims

The primary aim of this study is to understand and model a 2-alternative forced choice temporal bisection procedure, regardless of any extrinsic parameters, in both animal and human subjects. In order to achieve this aim, first I review the related literature to organize the experimental knowledge and spot inconsistencies in the existing explanations. Then, I explain the dynamics of this procedure by using a model that employs only the scalar property of timing and Bayesian learning. Contrary to the previous literature, this model uses two new approaches to explain the temporal bisection procedure: A) Temporal perception has a positively skewed distribution instead of a normal distribution, and B) A learning process is implemented at the level of a single trial to account for continuous updating of anchor duration perception throughout the procedure.

CHAPTER II

LITERATURE REVIEW

Initially, a very simple form of the temporal bisection task was used by Cowles and Finan (1941) with animal subjects, and then researchers tried to modify it to better understand the underlying mechanisms of time perception (Stubbs, 1968). Since the TIP directly represents subjective temporal perception, identifying its location in relation to the different intrinsic parameters of the task has become the most important challenge in the temporal bisection literature. Researchers have been studying the effect of different parameters of this task to address this concern for more than half a century. But due to the complexity of full factorial design, each of the studies investigated a subset of these parameters in a single experiment, which leaves open the question of their interactive effect. Consequently, explanations that holistically capture the dynamics of this procedure have not been developed.

In the following subsections, related temporal bisection studies are grouped by individual parameters to ease understanding of the current literature and generalization of the studies. Although the location of the TIP in animal and human literature is different, the effect of intrinsic parameters on the TIP is generally the same in both literatures. Finally, several leading theories and models of timing are reviewed and discussed in order to draw a better picture where the proposed model fits in the literature.

Range and Ratio of Anchor Durations

Platt and Davis (1983) showed that the range and ratio of anchor durations affect the location of the TIP and proposed conditions by which the TIP would be located at the GM of anchor durations for animal subjects. They experimented with a wide range of

anchor durations from 10 to 200 seconds and proposed that if the “Long” anchor duration is no more than four times the “Short” anchor duration, then the TIP will fall at the GM of the anchor durations. Allan (2002) has also shown that the range and ratio of anchor durations, together with the other intrinsic parameters, could bias researchers’ interpretation of the TIP; however, he found that the effect of these intrinsic parameters is not often consistent among individuals both within and across experiments. One of the most surprising phenomena in the temporal bisection task was documented by Siegel (1986): psychometric reversal on out-of-range durations. Siegel showed that the use of test durations that are out of the range of anchor durations not only could shift the location of the TIP, but also could cause a reversed pattern of response in rats for the out-of-range durations. In other words, contrary to the expectation, durations shorter than “Short” anchor duration and those longer than “Long” anchor duration were judged “Short” and “Long”, respectively, less often than anchor durations by animals. Although this psychometric reversal effect was later replicated by other researchers as well (Killeen & Fetterman, 1998; Castro et al., 2013), Siegel experimented with just two specific out-of-range durations, which leaves a lot of unanswered questions about the effect of the test durations range on the TIP location. For example, it is not clear why in the chosen durations, long out-of-range durations have more deviation from the anchor duration response than the short out-of-range durations; or why out-of-range durations shift TIP to the left.

Moreover, substantial differences in the range of durations could even engage a totally different neural system in the brain to process temporal information. For example, sub-second, interval or second-to-minute, and circadian timings are processed with different parts of the brain (Buhusi & Meck, 2005; Buhusi & Cordes, 2011). However, this

distinction is not very significant around the one-second range (Buhusi & Cordes, 2011); the human literature is fairly centered around the sub-second range due to the fact that this range is not confounded with counting. In contrast, since counting is not an issue in animal subjects, the animal literature is fairly centered around interval timing range. Thus, this range difference should be considered when comparing different studies.

In conclusion, the range and ratio of the anchor durations are factors of enough importance that any comparison in the literature without controlling for them could lack validity.

Spacing and Number of Test Durations

Raslear (1983) demonstrated that different distributions of intermediate durations could shift the TIP either to the left or right. Specifically, logarithmic spacing of intermediate durations shifts the TIP leftward in comparison to linear spacing, both in animal and human subjects (Raslear, 1985; Wearden & Ferrara, 1995). In general, the skewness in the distribution of test durations shifts the TIP in the opposite direction of said skewness (Brown et al., 2005). In other words, if the test durations are mostly chosen from durations that are closer to the short duration, then the TIP will be shifted towards the short duration; if the test durations are mostly chosen from durations that are closer to the long duration, then the TIP will be shifted towards the long duration. This also indicates that even the test durations that are chosen linearly, but presented with a non-uniform frequency, should shift the TIP towards the duration of higher presentation frequency. Although the effect of the spacing of test durations is shown frequently in the animal and human literature (Raslear, 1983, 1985; Wearden & Ferrara, 1995; Allan, 2002; Brown et al., 2005), there is no explanation for this phenomenon that also explains the effect of other

parameters at the same time.

Moreover, the number of test durations in a temporal bisection task is closely related to the way that test durations are distributed. Although the type of test duration spacing affects the location of the TIP, Siegel (1986) showed that the number of test durations does not affect the location of the TIP if the test durations in different conditions are chosen from the same distribution or spaced in the same manner. However, Siegel (1986) just tested 3, 5, and 7 test durations which leaves the effect of extreme cases like 1 or more than 10 test durations still unclear.

In conclusion, researchers should be considerate of the distribution and spacing of the test durations when comparing the TIP location in different studies, since information about the location of the TIP without these considerations can be misleading and incomplete.

Type of Response Reinforcement

In a comprehensive study of temporal properties of behavior (Catania, 1970), it is cogently argued that the way in which subjects respond in a behavioral task not only depends on the rate and temporal distribution of reinforcements, but also is heavily affected by the time between responses and subsequent reinforcements.

Specific to the temporal bisection task, Raslear (1985) demonstrated that different probabilities of reinforcement for correct responses to the anchor durations changes the location of the TIP. In this study, however, similarly to most of the other temporal bisection tasks, the correct responses for the test durations are left without any positive reinforcement. Although this method of reinforcing is often used by researchers, it should be considered that not being reinforced for the test durations will affect the way that

subjects update their perception of the anchor durations. In other words, in an environment in which some actions are rewarding (here, correct responses to the anchor durations), the actions without any consequences (here, correct responses to the test durations) can be considered as negative feedback. For example, assuming 2 and 8 seconds as the anchor durations, a “Short” response made by the subject to a 3 second duration which is not rewarded can cause the subject to update the perception of the short anchor duration to a shorter duration in order to compensate for the error. In the Methods section, for the sake of simplicity, any type of reinforcement that leads subjects to perceive that their response was or was not correct is referred to as positive or negative feedback respectively.

Reinforcement is an important concern in temporal bisection tasks, since awarding the intermediate durations will also result in other complications in the process by which the subjects update their memory of anchor durations. On the other hand, not rewarding at all will cause the extinction of learned temporal contingency.

However, one of the main differences in animal and human literature is the way that subjects are reinforced. In general, human participants receive a fixed amount of money or credit in order to complete the experiment, while animal subjects are usually deprived to 80% of their weight in order to have motivation for completing the task and receive food rewards (Poling et al., 1990). Any mistake in the task for animal subjects may mean a subjectively larger loss as compared to human participants. Thus, any differential motivation to learn from errors across species may lead to different learning rates in temporal bisection procedure, which will be discussed in the Methods section in more detail.

Thus, in conclusion, researchers should be considerate of the reinforcement policy

when designing an experiment, since it has a substantial impact on the way that subjects update their temporal perception. Furthermore, any theory or model that explains any mechanism in the temporal bisection task must consider each individual trial and the way that it affects the decision made in the next trials; therefore, theories that are not framed considering learning at the level of a single trial level lack validity

Leading Theories of Timing

Scalar Expectancy Theory (SET; Gibbon, 1977) and theory of Learning to Time (LeT; Machado, 1977) are two of primary and dominating theories in timing literature. SET that utilizes the Information Processing model of timing (Triesman, 1963), in learning phase of timing tasks, develops a normal distribution centered on to-be-learned duration and uses that fixed distribution in the test phase of the timing tasks. However, instead of continuous learning, SET introduces dynamicity to the model by adding noise in several ways such as implementing noisy Pacemaker and noisy Reference Memory access. On the other hand, LeT which is a more detailed version of Behavioral Theory of timing (BeT; Killeen & Fetterman, 1988), uses more behaviorally feasible process than SET in order to describe timing mechanism. In learning phase, LeT utilizes associative learning to link Behavioral States and Instrumental Responses and uses this association in the test phase to make appropriate responses. In essence, LeT and several other models of timing such as Multiple Time Scale (MTS; Staddon & Higga, 1999), Miall's model (Miall, 1989), Striatal Beat Frequency (SBF; Matell & Meck, 2004), SBF-Morris-Lecar (Oprisan & Buhusi, 2011), and Spectral Timing model (Grossberg & Schmajuk, 1989) utilize the concept of coincidence detection (Jeffress, 1948) with a single- or multi-layered neural network that tries to learn the transformation function of specific features to appropriate timing

responses. However, in the originally described version of all these models learning stops in the test phase of timing tasks or is not described in the test trials. Most of these models utilize random noise in the model in various ways to make it more dynamic.

In conclusion, the significance of dynamic temporal learning in the test phase and in particular test trials of timing tasks are undermined in the literature. Moreover, most of the timing models adjust for the dynamic learning with introducing random noise.

Summary

In sum, the GM and AM of anchor durations are widely accepted and experimentally supported locations for the TIP in animal and human literatures, respectively, controlling for the range and ratio of the anchor durations and spacing of the test durations (Reynolds & Catania, 1962; Stubbs, 1976, 1968; Church & Deluty, 1977). Moreover, the range and ratio of the anchor durations, spacing of the test durations, and policy of reinforcement for the correct or incorrect responses play a key role in determining the location of the TIP and subjective perception of the time.

Finally, although models in the timing literature have a learning element or process, most of them lack a learning process in the test phase of the timing tasks.

CHAPTER III

METHODS

In the following subsections, I first discuss the problems with assuming a normal distribution for temporal perception. Then, using the scalar property of timing, I obtain a positively skewed distribution for temporal perception, which agrees with experimental results better than a normal distribution. Second, using this distribution, I propose a model that uses only Bayesian learning to explain the discrepancy between the human and animal temporal bisection literature. In the proposed model, all the effects of intrinsic parameters on TIP location agree with experimental results. The structure of the proposed model can be understood through two stages: learning and decision. Explanation of the model includes the architecture of each stage and the dynamics by which these pieces work together.

Normal Distribution for Temporal Perception

One of the major assumptions, or at least modeling tool, in the time perception literature is the normality of temporal perception (Gibbon, 1977). In other words, when a subject learns a duration, a normal probability distribution centered on that duration is assumed for how probable it is that the subject perceives other durations as the learned duration. Width of this distribution depends on the subjective error of temporal perception, which can be estimated experimentally. For example, Figure 1 shows three normal distributions with different standard deviations for temporal perception of one second duration. Temporal perception distributions are max-normalized in order to have maximum probability for the perception of learned duration, and width is scaled by the magnitude of learned duration. Equation 4 shows the max-normalized normal distribution for duration with magnitude of μ and error of σ .

$$N(x, \mu, \sigma) = e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (4)$$

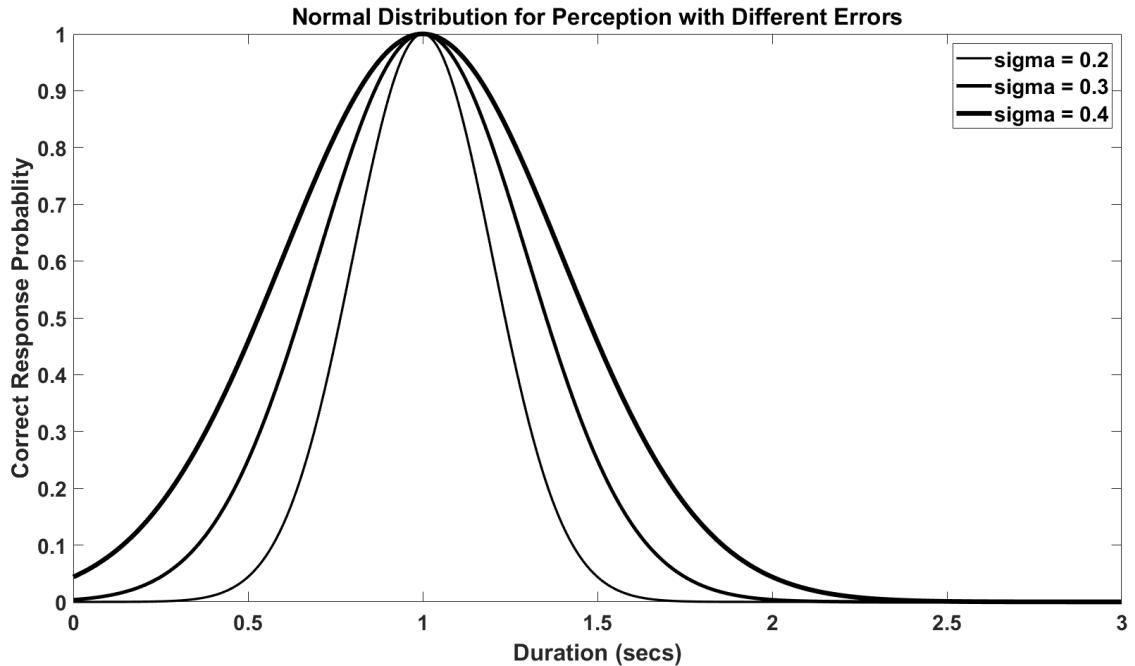


Figure 1. Three normal distributions for temporal perception of a one second duration with different perceptual errors.

Y-axis shows the probability that a subject perceives a specific duration as a one second duration.

A normal distribution for temporal perception might seem the most parsimonious assumption, but it is one of the least feasible assumptions because of the following two reasons. First, since zero or negative durations are not defined perceptually, temporal perception should have a positive distribution, while normal distributions cover zero and negative durations as well. In other words, it assumes a non-zero probability for zero or negative durations to be perceived as a specific duration. Secondly, it has been shown

experimentally that temporal perception has a positively skewed distribution (Buhusi & Meck, 2005), while the normal distribution is a symmetric distribution. These infeasibilities of assuming a normal distribution for temporal perception may cause misunderstanding in the temporal bisection literature by affecting the location of the TIP.

Moreover, considering the fact that the perceptual distributions' cross-point is the duration that subjects perceive as the short anchor duration as equally as the long anchor duration, Staddon and Higa (1999) argue that assuming a normal distribution for temporal bisection locates the TIP in the HM of the anchor durations (see Figure 2). Later in this thesis, I will demonstrate how any change in the shape of perceptual distributions will change the location of the TIP.

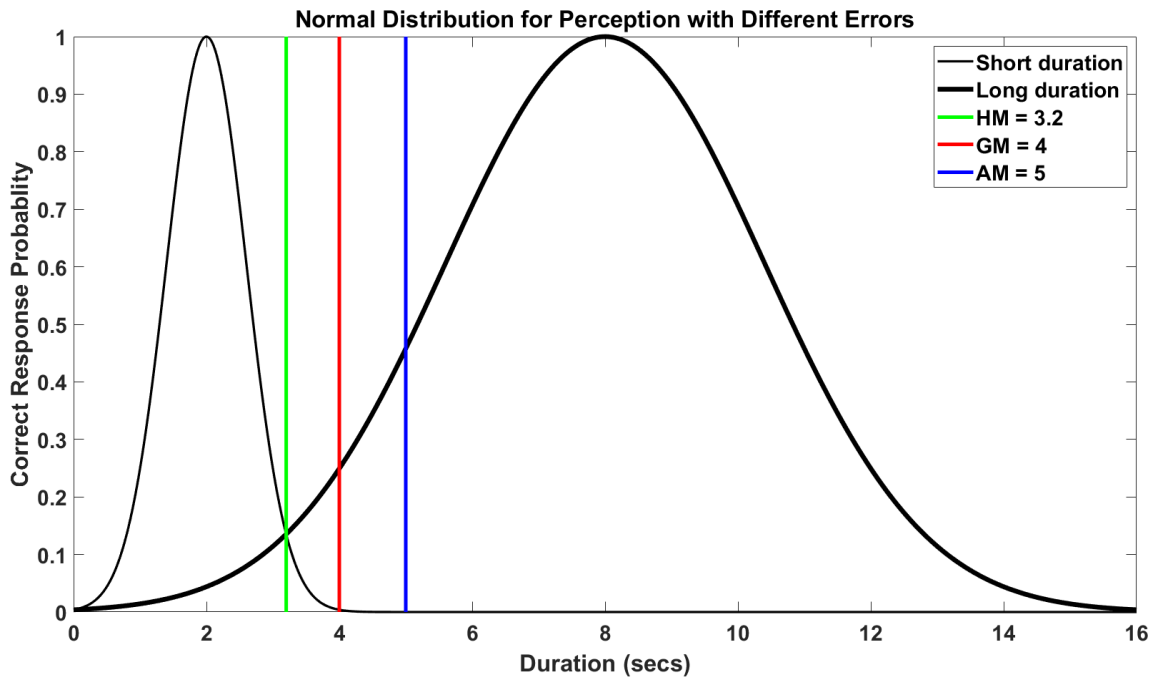


Figure 2. Assuming normal distributions for the perception of anchor durations locates the TIP in the HM of the anchor durations.

The cross-point of the perceptual distributions for anchor durations is the duration

that is perceived by subjects equally as the short and long anchor duration. The HM, GM and AM of the anchor durations are shown with vertical lines in different colors for the sake of comparison.

Positively Skewed and Scalar Distribution for Temporal Perception

In order to discuss the location of the TIP in the temporal bisection task, it is necessary to clarify the perceptual distributions for the short and long durations. This will help to find the initial location of the TIP before attempting to model the procedure. Although intensive experimental data are needed to obtain the precise distributions of perceptions, we can use well-established results from the available literature as heuristics to improve these distributions. Currently, normal distributions with scalar standard deviations are assumed for temporal perception of the anchor durations.

I improved these distributions by using the scalar property of timing to obtain positively skewed distributions. For the purpose of simplicity, I discuss mainly the perceptual distribution for one second duration here; however, perceptual distribution for other durations is simply a scaled version of the perceptual distribution for one second duration.

In order to find the perceptual distribution of one second duration, the probability by which a duration is judged as one second should be computed for all durations. This probability is computed as the probability by which one second is judged to be a specific duration. Thus, the cross point of one second duration and scaled normal distributions centered on different durations were used to find these probabilities (see Figure 3). Then, these cross-points or probabilities were used to build the perceptual distribution of one

second duration (see Figure 4, top panel).

The width of these normal distributions are computed based on Scalar property of timing. With the assumption that ε is the standard deviation of the normal distribution centered on one second (referred to as absolute error hereafter), the scalar property of timing entails that the standard deviation of a distribution centered on t to be $t * \varepsilon$.

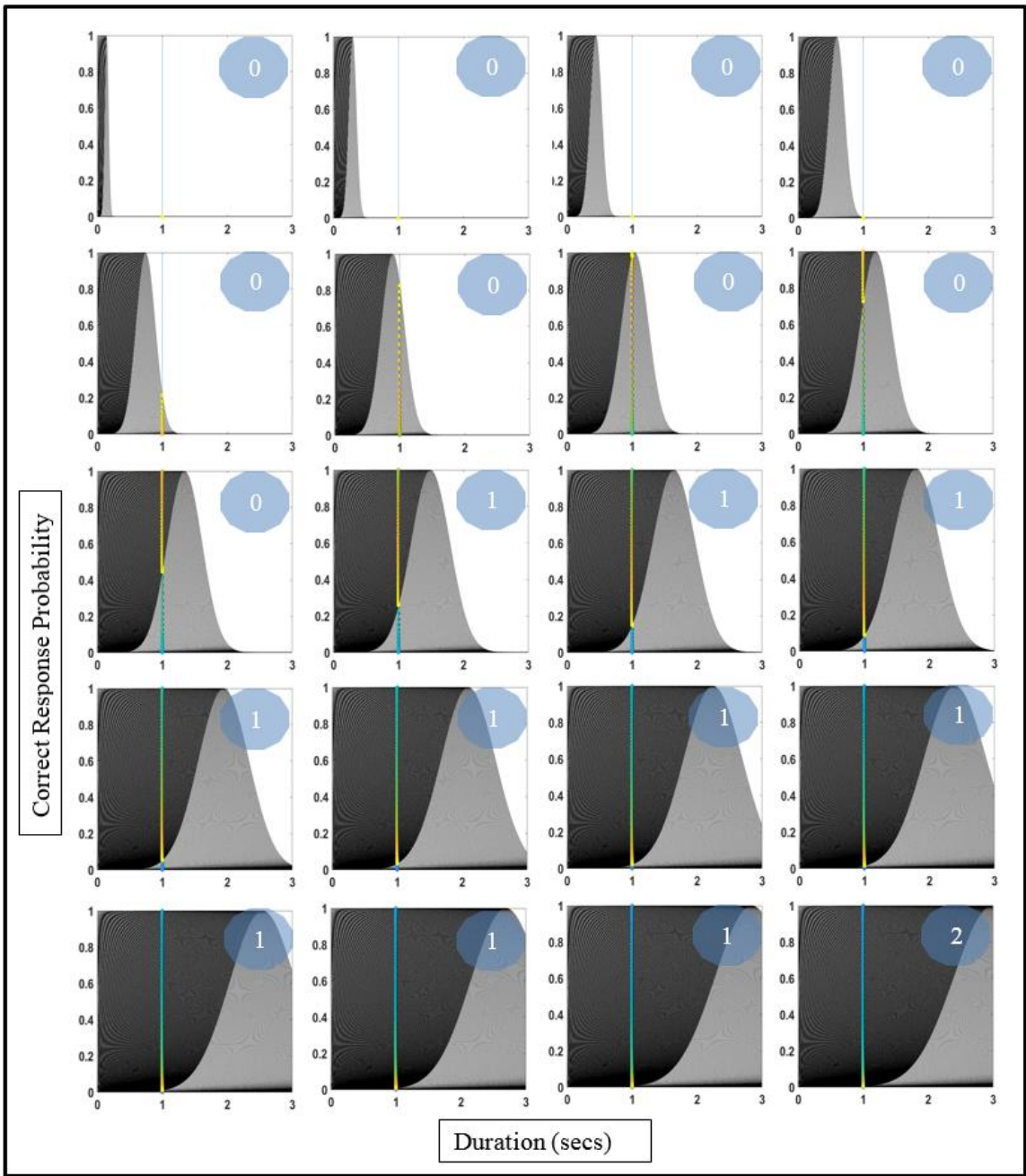


Figure 3. Cross-point of one second duration and 20 scaled normal distributions.

These cross-points are the probabilities by which one second duration is perceived as the center of normal distributions. Horizontal axis shows time in seconds and vertical axis shows the probability.

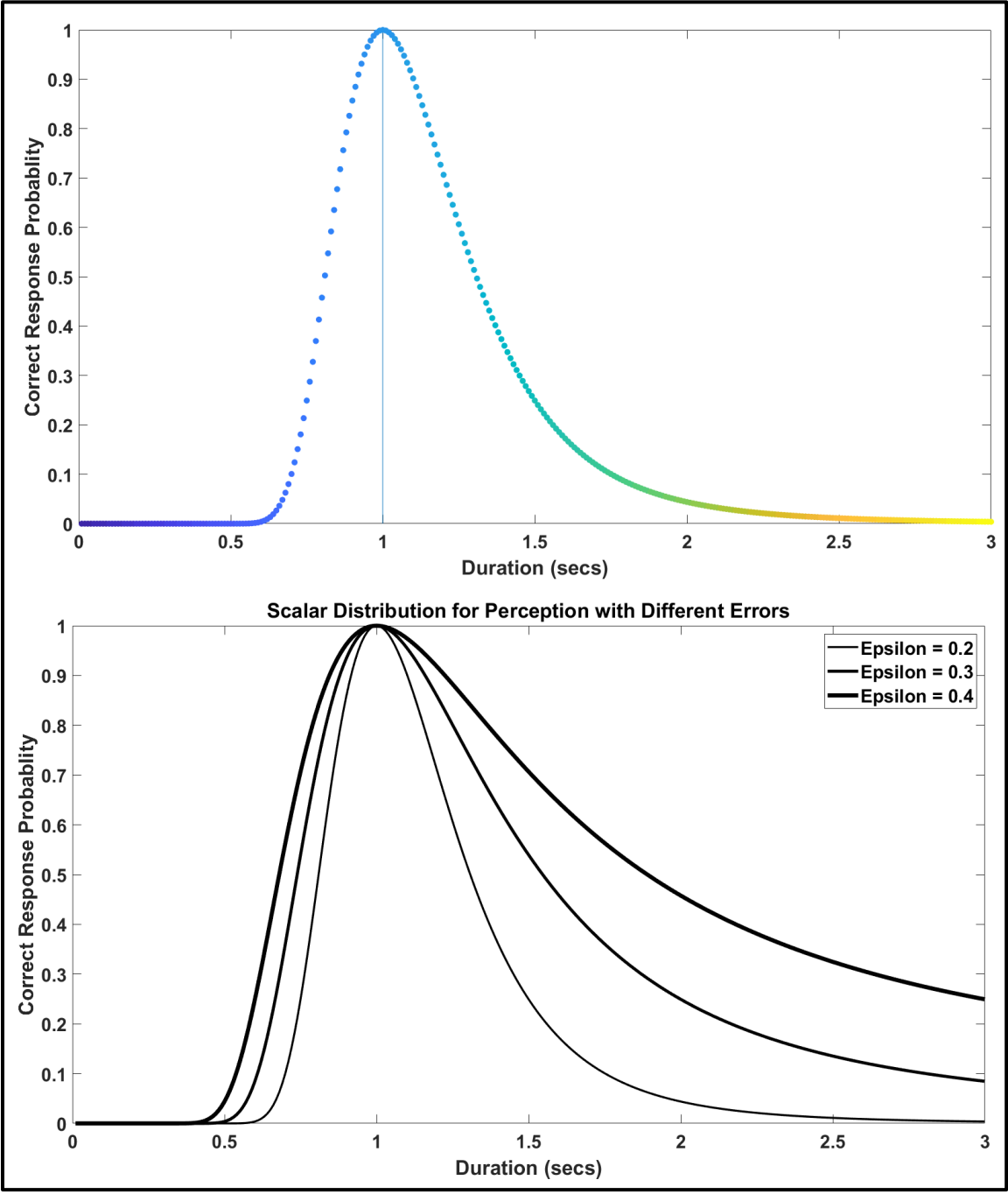


Figure 4. Positively skewed and scalar distributions for temporal perception of one second duration.

Top panel is the concatenation of cross-points from Figure 3 in order to demonstrate the process of obtaining a positively skewed and scalar distribution for temporal

perception of one second duration. Bottom panel shows three positively skewed and scalar continuous distributions with different absolute errors.

In general, in order to find the scalar perceptual distribution for T seconds duration (see Equation 6), values in Equation 5 should be plugged in the max-normalized normal distribution (see Equation 4).

$$\mu = t, \quad \sigma = \varepsilon * t, \quad x = T \quad (5)$$

$$P(t, T, \varepsilon) = e^{\frac{-(T-t)^2}{2(\varepsilon t)^2}} \quad (6)$$

Although this distribution might not exactly match the real distribution of temporal perception, I used it because of the following reasons: A) it is a more reasonable and feasible assumption than normal distribution in modeling temporal perception, B) it demonstrates how the shape of a distribution for temporal perception could affect conclusions of a model concerning the location of the TIP, C) it explains the location of the TIP in both human and animal subjects if a learning process is added to the model.

Considering the fact that temporal perception distribution is positively skewed, Figure 5 shows that if instead of normal distribution, the obtained perceptual distribution is used for anchor durations, the TIP shifts to the AM of the anchor durations. However, in general, any change in the shape of perceptual distributions could change the location of the TIP.

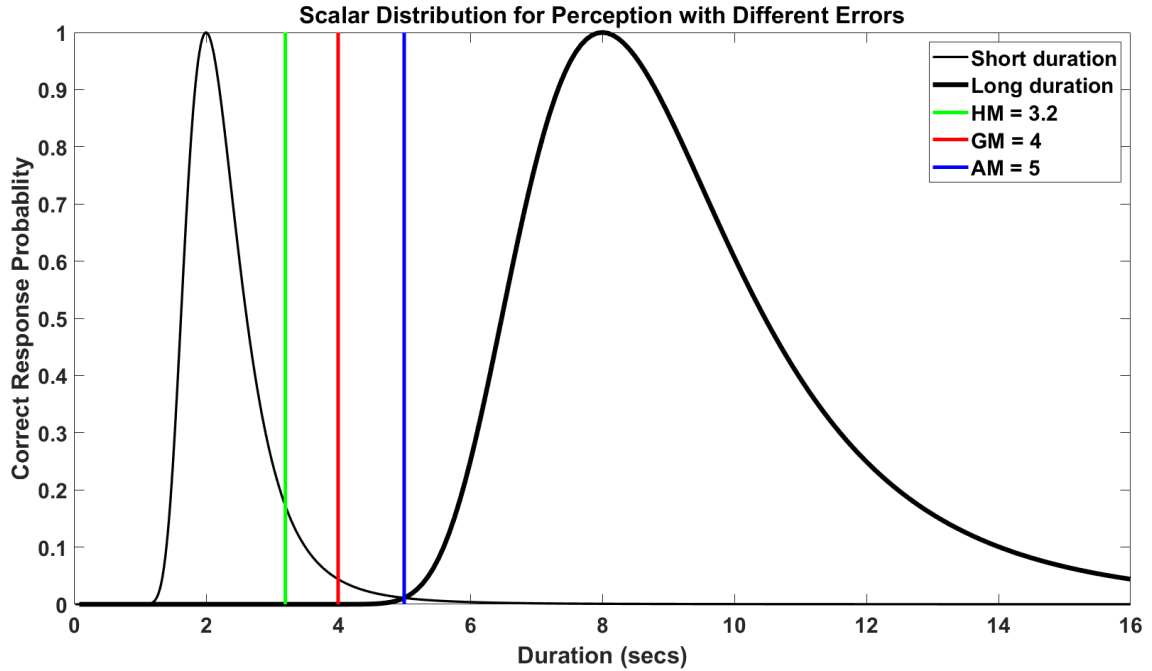


Figure 5. Assuming the obtained positively skewed distribution for the perception of anchor durations locates the TIP in the AM of the anchor durations.

The cross-point of the perceptual distributions for the anchor durations is the duration that is perceived by the subject equally as the short and long anchor duration. The HM, GM and AM of the anchor durations are shown with vertical lines in different colors for the sake of comparison.

Architecture of the Model

If we assume that subjects develop perceptual distributions for anchor durations in the learning phase of the temporal bisection task and keep them until the end of the task, the location of the TIP should be just the cross-point of perceptual distributions. The position of this thesis is that this assumption is valid for human participants but not for animal subjects. In order to train animal subjects for temporal bisection, researchers often

gradually deprive them of food until they reach approximately 80% of their free-feeding weight (Poling et al., 1990; Stubbs, 1968). On the other hand, human participants are usually received a set amount of money or credit for completing the task. Thus, comparatively, animal subjects have a greater subjective loss in any mistake in the task as compared to human participants. In other words, any single mistake in the task is critical for animals and can cause them to update their temporal perceptions to compensate for the error.

Having this argument in mind and using positively skewed perceptual distributions, I developed a model that learns from any single trial. This learning process is parametrized with learning rates such that no learning locates the TIP in the AM of the anchor durations, while a non-zero learning rate shifts the TIP to the left towards the GM of the anchor durations.

This model departs from the previous computational modeling of time perception because of the following reasons: A) it has a single-trial level learning process in all stages of the task, and B) it uses a positively skewed distribution for temporal perception of anchor durations for which the benefits have already been discussed.

Learning

Bayesian learning is one of the most common methods of learning that is widely used to explain behavior and actions (Clark, 2013). Using Bayesian learning, the proposed model continuously updates the perception of the learned anchor durations by any exposure to a duration which is to be judged. In a general sense, if the response made by the model has positive feedback, the model updates the perception of the related anchor duration to a perception closer to that of the presented duration; if the response made by the model has

negative feedback, the model updates the perception of the anchor durations to perceptions that in the future trials it is less likely that the model makes the same response for the same duration. For example, assuming 2 and 8 seconds as the anchor durations, a “short” response made by the model to a 3 second duration that has no positive feedback will cause the model to update the perception of the anchor durations to shorter durations in order to compensate for the error. In other words, it will be less probable to make the same choice for the presented duration in the future trials.

The learning process in the model is implemented by weighted averaging of the prior perception and current estimation of anchor durations. Specifically, two learning rates are considered for the model: positive learning rate (referred to as α hereafter) and negative learning rate (referred to as β hereafter). α is used when the model makes a response that has positive feedback, and β is used when the model makes a response that has negative feedback. Two learning rates are implemented in order to have the possibility of modeling conditions in which absolute values of reward and loss are not the same.

In case of positive feedback, the test duration (t) is considered as the current estimation of the anchor duration; and the updated perception is the weighted average of prior and current perception with the weight of $1-\alpha$ and α respectively. See Equation 7 for if the response made by the model is "Short" and t is equal to the short anchor duration and Equation 8 for if the response made by the model is "Long" and t is equal to the long anchor duration.

$$\hat{s} = (1 - \alpha) * \hat{s} + \alpha * t \quad (7)$$

$$\hat{l} = (1 - \alpha) * \hat{l} + \alpha * t \quad (8)$$

Where t denotes the presented duration and \hat{s}, \hat{l} denote perception of short and long anchor durations.

The same logic applies to negative feedback, but the $1-\beta$ and β are used for weighted averaging and the current estimation of the anchor durations is computed based on the certainty of the made response. The certainty of the response is computed as the ratio of the test duration's distance to the anchor duration over half the distance between the anchor durations (see Equation 9). This ratio is zero when the duration is exactly in the middle of the anchor durations, meaning that the made response is an outcome of a 50-50 probability; and it increases proportionally towards one as the test duration becomes closer to the related anchor duration.

$$Certainty = \frac{(t - \hat{s})}{0.5 * (\hat{l} - \hat{s})} \quad (9)$$

See Equation 10 for update rules if the response made by the model is "Short" and t is not equal to the short anchor duration and see Equation 11 for update rules if the made response by the model is "Long" and t is not equal to the long anchor duration.

$$\begin{aligned} \hat{s} &= (1 - \beta) * \hat{s} + \beta * (\hat{s} - \hat{s} * Certainty), \\ \hat{l} &= (1 - \beta) * \hat{l} + \beta * (\hat{l} - \hat{l} * Certainty) \end{aligned} \quad (10)$$

$$\begin{aligned} \hat{s} &= (1 - \beta) * \hat{s} + \beta * (\hat{s} + \hat{s} * Certainty), \\ \hat{l} &= (1 - \beta) * \hat{l} + \beta * (\hat{l} + \hat{l} * Certainty) \end{aligned} \quad (11)$$

However, the model has such structural flexibility that any other policy for updating the perception could be implemented and used. For example, different methods can be

used to compute the certainty of the made response and current estimation of the anchor durations.

Additionally, there is a decay rate parameterized as λ for the learning rates that can be set to anything between zero to one. In each trial, the current learning rates are multiplied by $1 - \lambda$ (see Equation 12). If the decay rate is set to zero, the learning rates would stay the same for all the trials, but if it is set to a number more than zero, the model learns relatively more from the first trials than the last trials.

$$\alpha = \alpha * (1 - \lambda), \quad \beta = \beta * (1 - \lambda) \quad (12)$$

This continuously updated perception for the anchor durations will be used in the decision stage. In other words, crucially, in each point in time the model has a new perception of the anchor durations, and any presented duration will be compared to these current perceptions rather than the fixed and initial perceptions. The proposed model implemented on a single trial basis is capable of employing any type of update rules considering different types of reinforcements or different given instructions and trainings.

In this model, the initial prior perceptions of anchor durations are assumed to be centered on the anchor durations. In other words, model assumes that the subjects perfectly have learned the anchor durations by the end of learning phase of the task. Although the prior perceptions of the anchor durations are initialized by the values of anchor durations, this model could be independently extended to the learning phase of temporal bisection as well. In order to describe the dynamic of learning phase, the prior perceptions of the anchor durations should be initialized to reasonably random values and get tuned gradually over the training trials.

Decision

Using the continuously updated perception of the anchor durations, the model makes a probabilistic response to the presented durations to be judged. In other words, if the presented duration is more probable to be perceived as the short than the long anchor duration, then it is more probable that the model makes a “Short” response than a “Long” response. However, the structural flexibility of the model allows researchers to implement different decision rules to investigate other possibilities.

The response of the model for any test duration shorter than the short anchor duration or longer than the long anchor duration is “Short” and “Long”, respectively. However, experimentally this is not the case, and the subjects have a reversed response for such out-of-range durations (Siegel, 1986). In other words, subjects have a threshold after which they begin to change their decision about the length of out-of-range durations. Since the decision process in the out-of-range durations is not experimentally explored and studied, it is not implemented in this model and only the regular conditions are used to verify the results of the model. Future studies could improve the model for the out-of-range durations based on understanding of the decision process for these durations.

Dynamics of the Model

After the initial learning phase of the temporal bisection procedure, the model develops two perceptual distributions centered on the anchor durations with scalar errors (see Figure 5). In the testing phase of the procedure, on any individual trial, prior perceptions of the anchor durations are used to make a response as explained in the decision stage of the model. After the response has been made, based on the received feedback, the model updates the distributions’ center for the perception of the anchor durations as

explained in the learning stage. In summary, the model always keeps updated perceptions of anchor durations that help to bisect the presented durations in any trial and updates them based on the received feedback (see Figure 6).

After all the trials are presented and responses are recorded, a psychometric function of responses can be generated. Although the sequence of trials affects responses made by the model, it does not statistically affect the psychometric function or the location of the TIP.

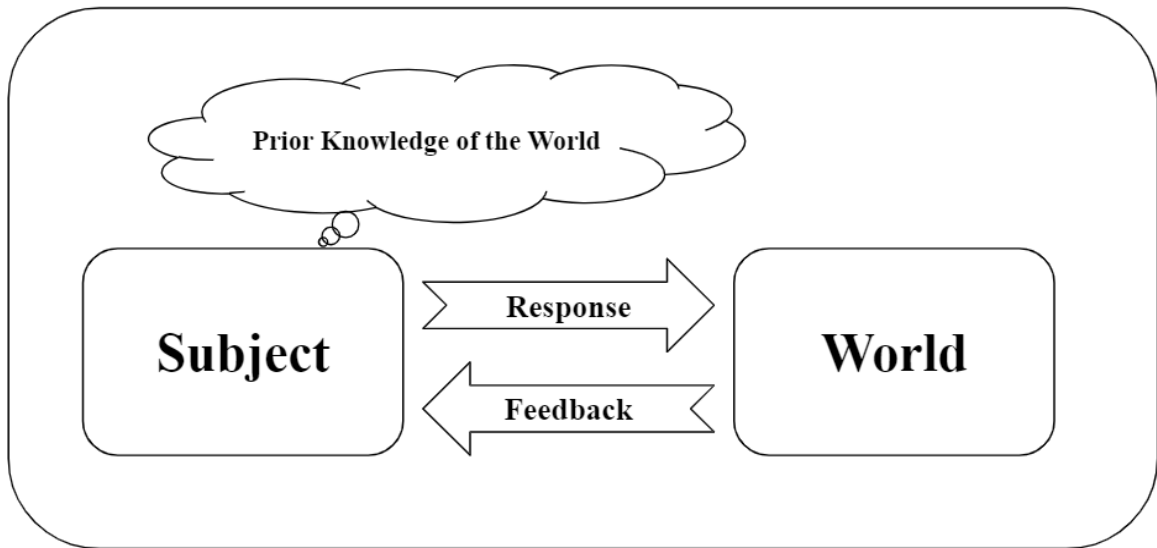


Figure 6. Diagram of a Bayesian model.

Prior knowledge of the world is constantly updated based on received feedback from the world, and a response is made based on the current knowledge of the world and presented duration.

CHAPTER IV

RESULTS

Using the data from Siegel (1986), the model is run through different conditions and the results are reported in the following subsections. Similar to most temporal bisection experiments, only the correct responses to the anchor durations are positively reinforced (a positive feedback is given to the model). However, as already has been discussed, responses made for test durations between the anchor durations are considered to have perceived any lack of positive feedback as negative feedback, since it is crucial for animal subjects not to miss a food reward. Moreover, learning rates are set to values from the results of the model in the first experimental condition and are kept the same for the rest of the conditions.

Learning vs No Learning

To the best of my knowledge, the computational models set forth in the literature on temporal bisection ignore the learning dynamics on a single trial basis, specifically in testing phase. Here, the model is run with and without the learning process to demonstrate how continuous learning affects the location of the TIP. As demonstrated in Figure 7, when there is no learning process, the perception of the anchor durations remains the same through all the trials; however, it is constantly updated when a learning process is applied. In the absence of any learning process, the TIP falls in the AM of anchor durations, while a learning process with specific learning rates shifts the TIP from the AM to the GM of anchor durations (see Figure 8). As reported in Table 1, Task parameters are chosen from Siegel (1986), and free parameters are chosen in a way that the results of the model match with the first experimental condition and are kept the same for the rest of the conditions.

Table 1*Parameters that are used in “Learning” vs “No Learning” conditions*

| | |
|--|---|
| Task Parameters: | |
| Short Duration | 2 secs |
| Long Duration | 8 secs |
| Test Durations | [2 2.4 2.8 3.3 4 4.8 5.7 6.8 8] |
| Number of Trials for Test Durations | [70 20 20 20 20 20 20 20 70] |
| Runs | 100 |
| Free Parameters: | |
| Absolute Perception Error (ϵ) | 0.2 secs |
| Positive Learning Rate (α) | 0.1 (zero for “No Learning” condition) |
| Negative Learning Rate (β) | 0.25 (zero for “No Learning” condition) |
| Learning Decay Rate (λ) | 0.02 (zero for “No Learning” condition) |

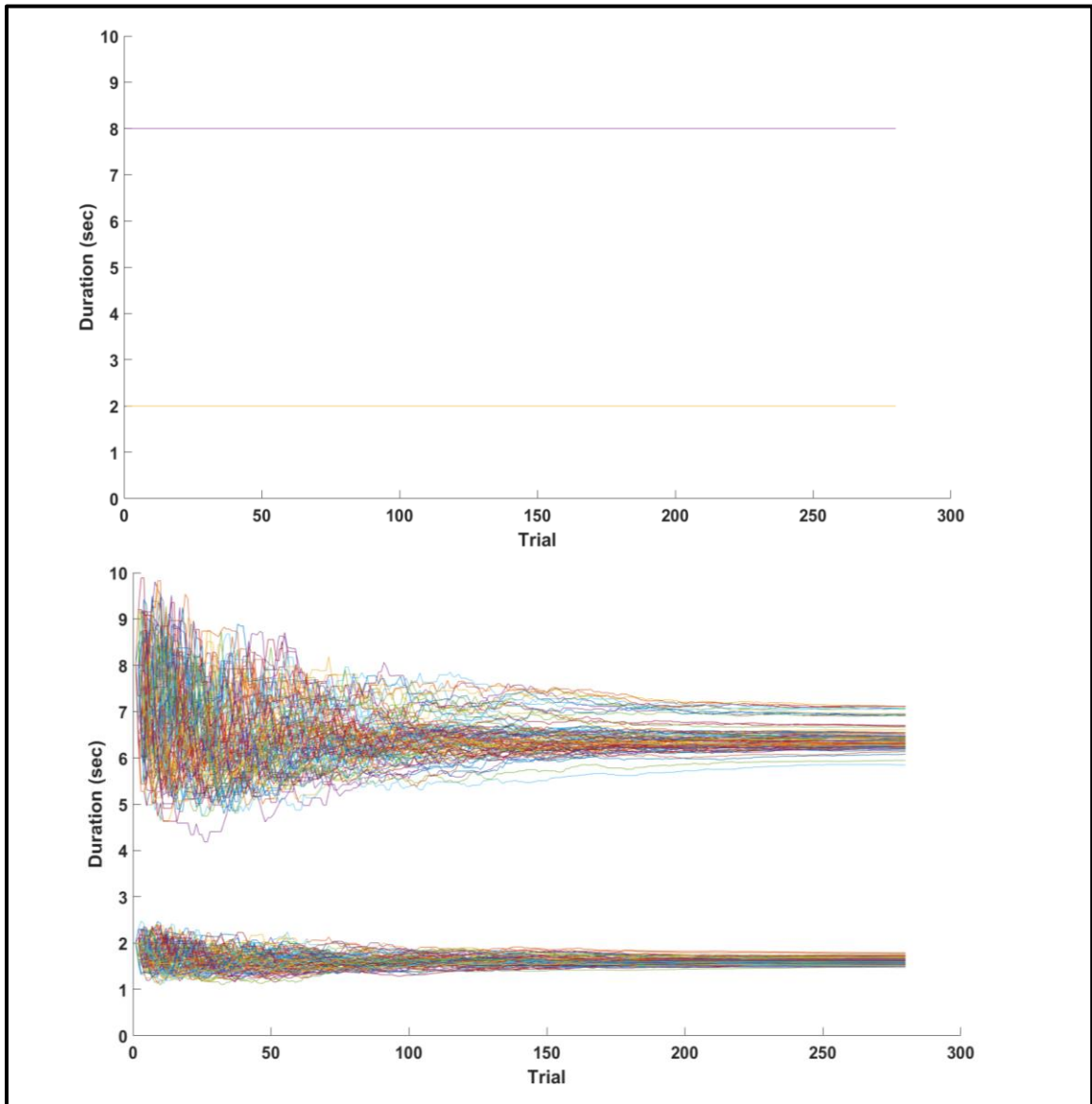


Figure 7. Center of the perceptual distributions for anchor durations over trials.

In the top panel the learning rates of the model are set to zero and consequently the center of perceptual distributions are remained the same over the trails. In bottom panel, the learning rates of the model are set to non-zero values and consequently the center of perceptual distributions varies over the trials. Different lines in the bottom panel represent different runs of the model.

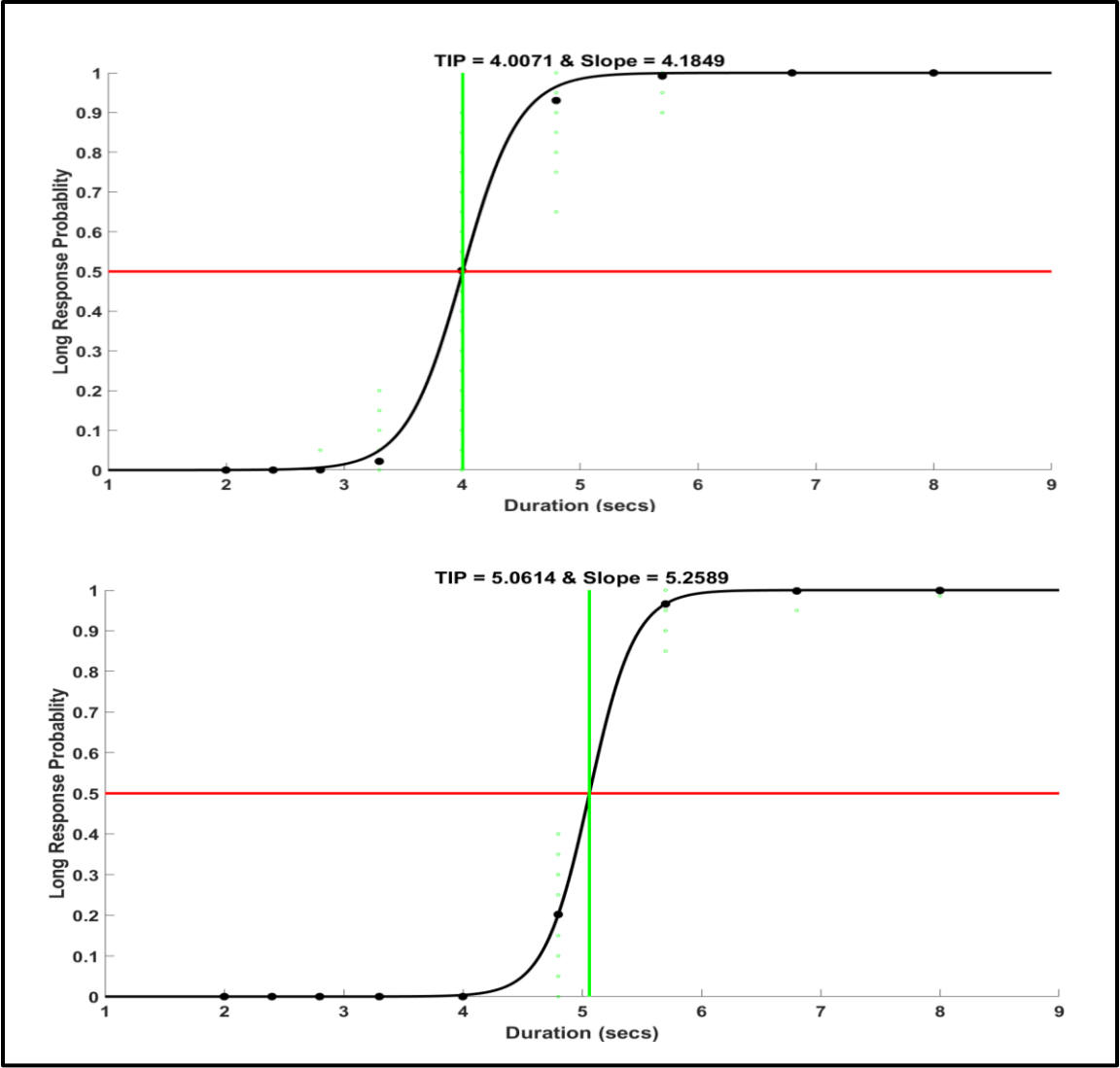


Figure 8. Psychometric function of responses with learning (top panel) and without learning (bottom panel).

Why Geometric Mean?

The fact that the learning rates are free parameters in the model explains the variance of the TIP among different individuals. In other words, individuals with a greater learning rate have a lower TIP as compared to subjects with a lesser learning rate; Figure 9 and Figure 10 show the relationship between positive and negative learning rates and

location of the TIP (all the parameters other than learning rates are kept the same as in Table 1).

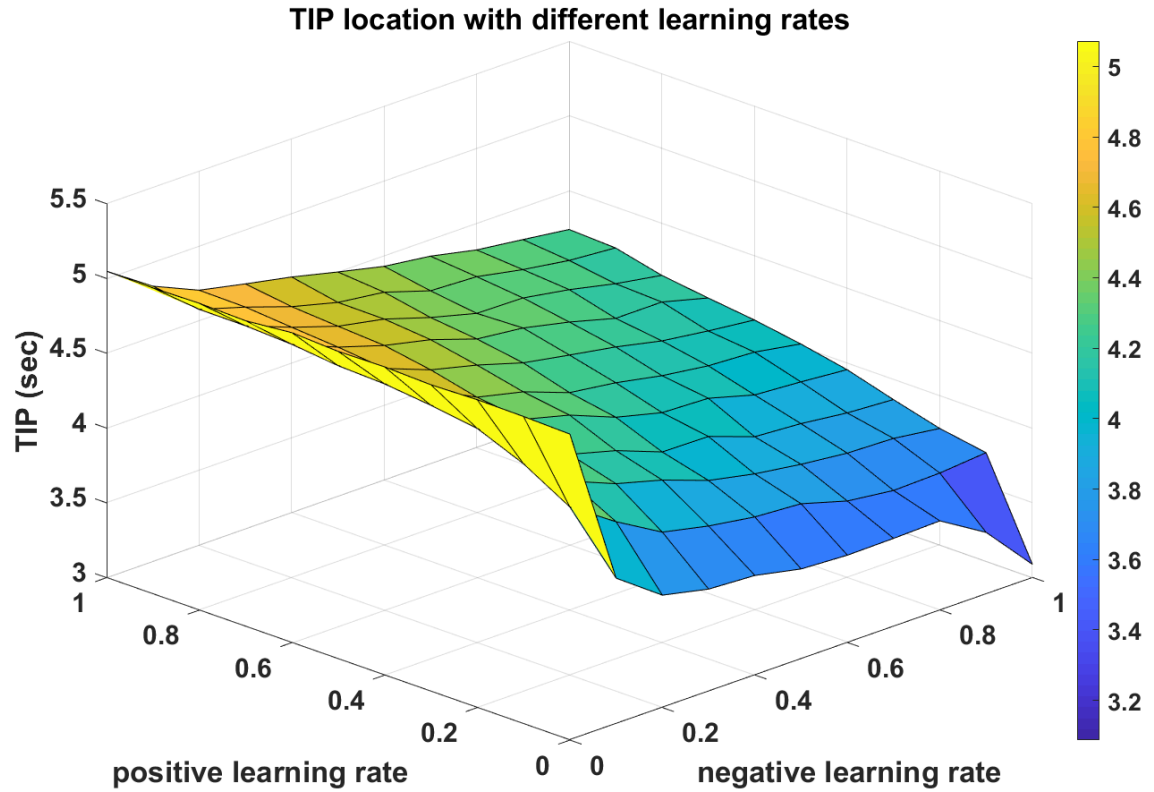


Figure 9. The relationship between positive and negative learning rates and the location of the TIP in a 3D plot.

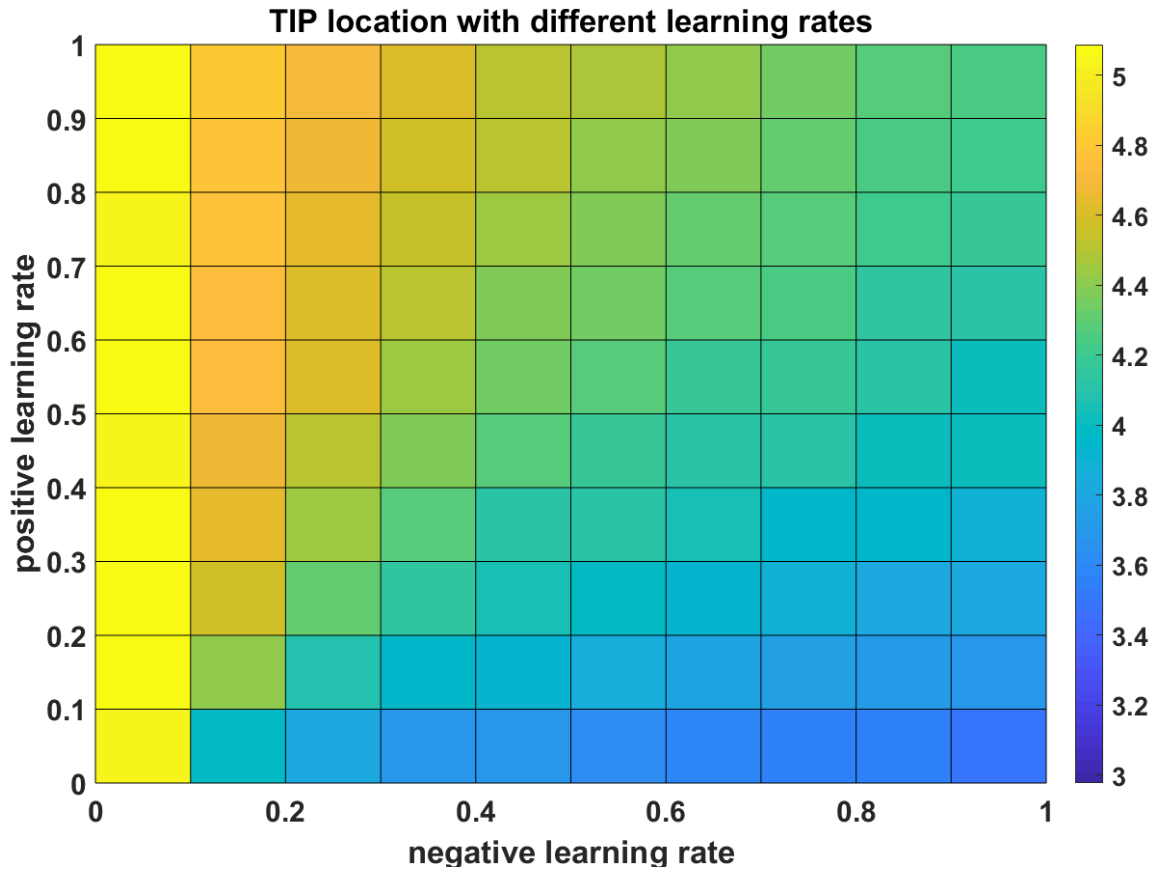


Figure 10. The relationship between positive and negative learning rates and the location of the TIP in a 2D plot.

However, if the positive and negative learning rates are kept roughly the same (see diagonal line in Figure 10), the TIP always falls on the GM of anchor durations. The reason for this is that the GM of anchor durations is the median of logarithmic test durations. Equation 13 shows n points spaced logarithmically between two arbitrary numbers x and y :

$$e^{\log x}, e^{\log a + 1\beta}, e^{\log a + 2\beta}, \dots, e^{\log a + i\beta}, \dots, e^{\log y}$$

$$\text{where } \beta = \frac{(\log y - \log x)}{n} \quad (13)$$

Equation 14 shows that the median of these n points is equal to the geometric mean of x and y :

$$\begin{aligned}
 \text{Median}(x, y) &= e^{\log x + \frac{n}{2}\beta} = e^{\log x} * e^{\frac{n}{2} * \frac{(\log y - \log x)}{n}} \\
 &= x * e^{\frac{(\log y - \log x)}{2}} = x * \sqrt{e^{(\log y - \log x)}} \\
 &= x * \sqrt{\frac{e^{\log y}}{e^{\log x}}} = x * \sqrt{\frac{y}{x}} \\
 &= \sqrt{x * y} = GM(x, y)
 \end{aligned} \tag{14}$$

Through the learning process, testing with any duration closer to the short anchor duration shifts the perception of anchor durations to the left, and testing with any duration closer to the long anchor duration shifts the perception of anchor durations to the right. The mid-point of anchor durations is the point by which left- and right-moving updates of anchor durations' perception are equal. Thus, perceptions of anchor durations shift until the TIP is located at the GM of anchor durations.

Logarithmic vs Linear Spacing

As it is widely shown in the literature, logarithmic spacing of test durations shifts the TIP to the left or, in other words, linear spacing of test durations moves the TIP to the right. Here, both linear and logarithmic spacing of test durations (see Table 2; all the parameters other than test durations are kept the same as in Table 1) were used to demonstrate this phenomenon (see Figure 11). This phenomenon happens because of the distribution of test durations; in linear spacing there are an equal number of test durations shorter and longer than the AM of anchor durations, and thus the AM of anchor durations is a stable point for the TIP in the learning process. On the other hand, in logarithmic

spacing, the GM of anchor durations has this mid-point property. In other words, when test durations spaced logarithmically, there are an equal number of test durations that are shorter and longer than the GM of anchor durations.

Table 2*Durations and number of trials for linear and logarithmic spacing of test durations*

| | |
|---|-----------------------------|
| Linear Test Durations | [2 3 4 5 6 7 8] |
| Number of Trials for Linear Test Durations | [50 20 20 20 20 20 50] |
| Logarithmic Test Durations | [2 2.52 3.18 4 5.04 6.35 8] |
| Number of Trials for Logarithmic Test Durations | [50 20 20 20 20 20 50] |

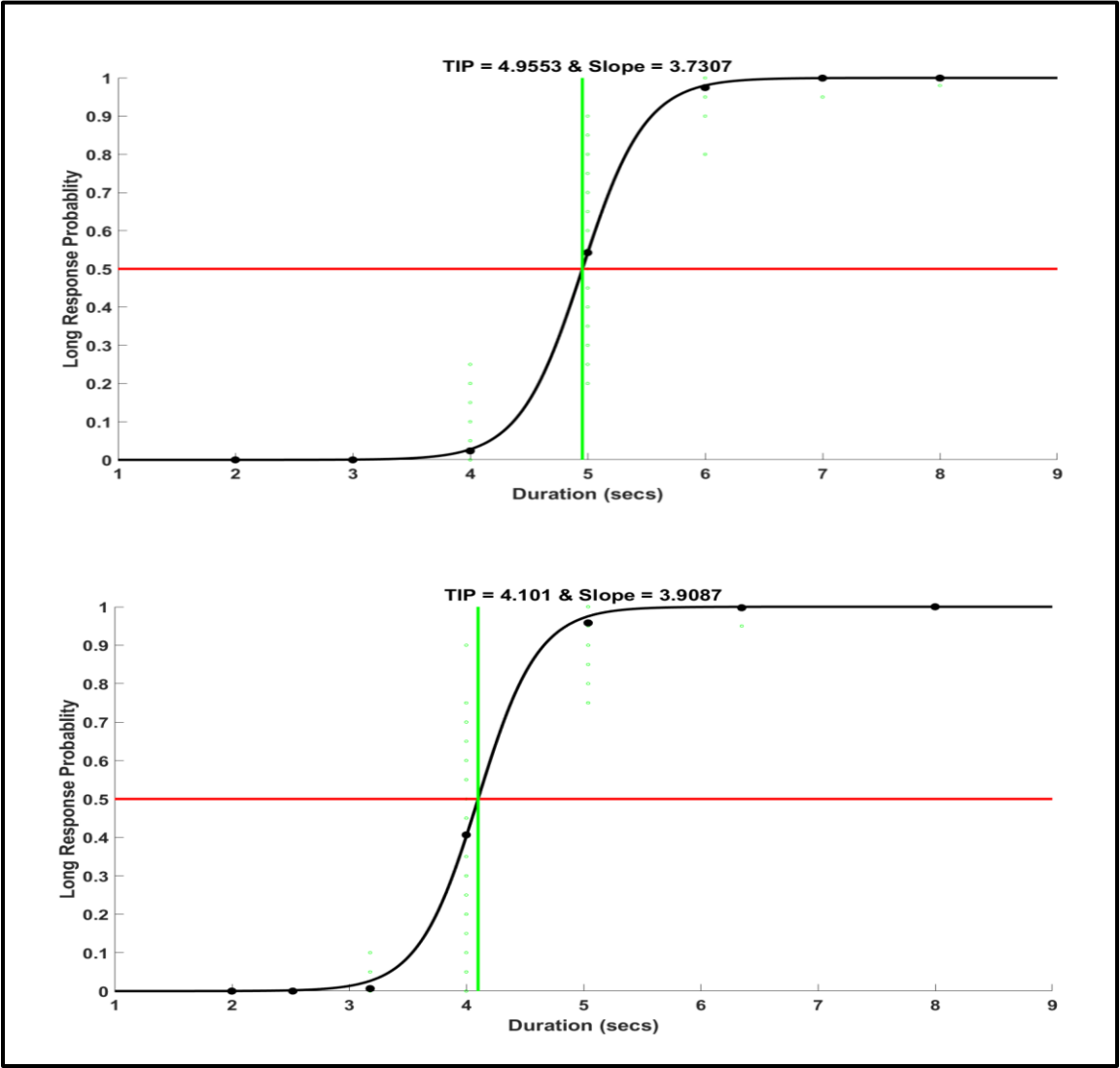


Figure 11. Psychometric function of responses using linear (top panel) and logarithmic (bottom panel) spacing of test durations.

Number of Intermediate Durations

Siegel (1986) showed that the number of test durations does not significantly affect the location of the TIP as long as durations are chosen from the same distribution. Here,

the same parameters from Siegel (1986) are used to demonstrate the effect of number of test durations on the TIP (see Figure 12 and Table 3; all the parameters other than number of test durations are kept the same as in Table 1). Interestingly, similar to the experimental results, there is a 0.2 secs difference in the location of TIPs.

Table 3

Durations and number of trials for three and seven test durations conditions.

| | |
|---------------------------------------|---------------------------------|
| Test Durations - 3 Pints Condition | [2 2.8 4 5.7 8] |
| Number of Trials for 3 Test Durations | [30 20 20 20 30] |
| Test Durations - 7 Points Condition | [2 2.4 2.8 3.3 4 4.8 5.7 6.8 8] |
| Number of Trials for 7 Test Durations | [70 20 20 20 20 20 20 20 70] |

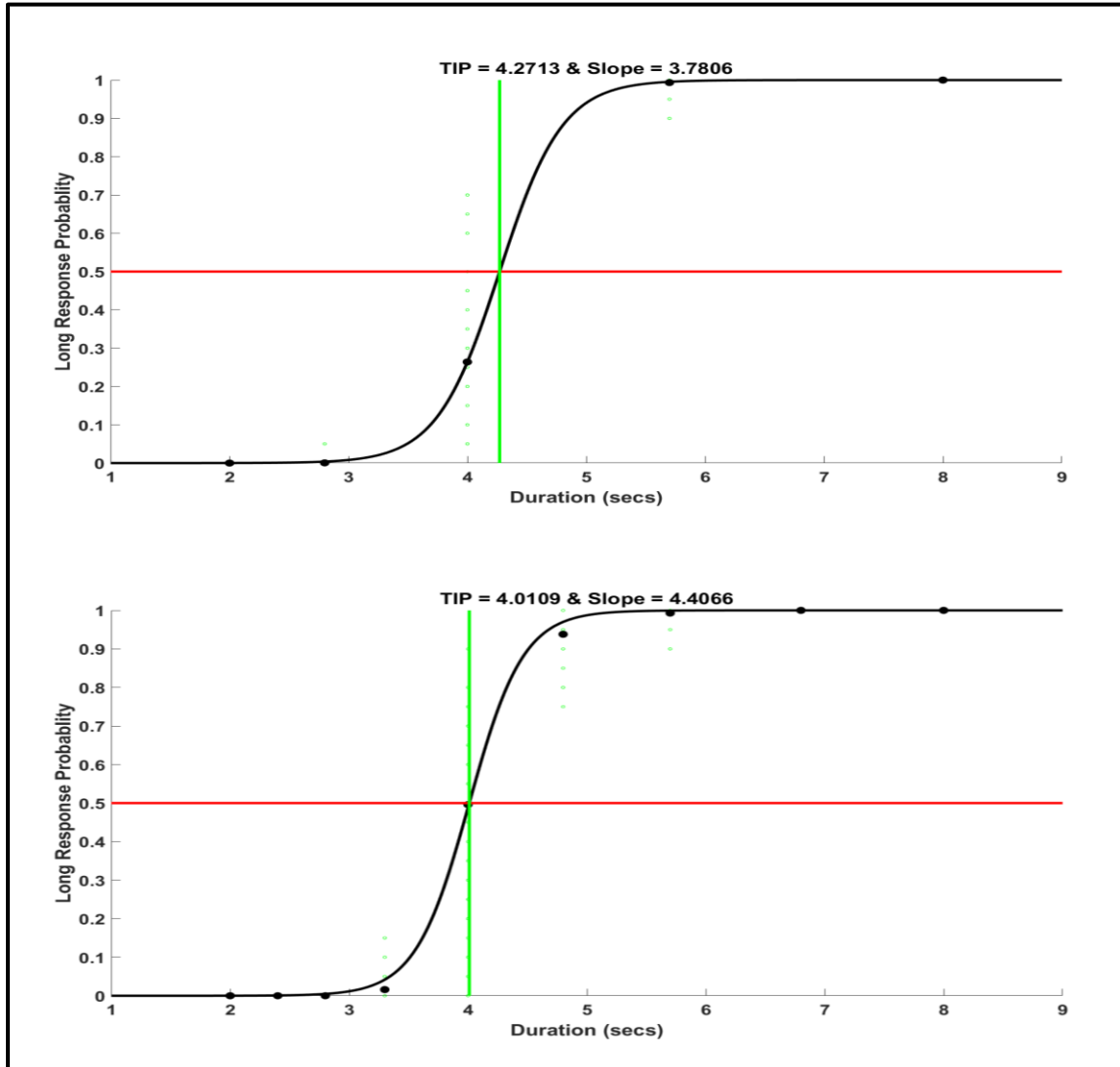


Figure 12. Psychometric function of responses using 3 (top panel) and 7 (bottom panel) test durations.

CHAPTER V

DISCUSSION

In this thesis, I identified two problems in the way that the temporal bisection procedure is modeled and understood in the literature. First, a normal distribution is usually assumed for the perception of anchor durations, while experimentally it is shown that the distribution of temporal perception is positively skewed. I demonstrated that this assumption of normality for temporal perception biases our understanding of the TIP and how a positively skewed distribution could help marry the computational and experimental literatures. Secondly, the importance of a learning process at the single-trial level, specifically in the testing phase of the temporal bisection procedure, is usually undermined in the literature. I demonstrated how a learning process could affect the location of the TIP. By helping solve these two problems, the proposed model better merges the animal and human literatures, which have often remained divorced for decades.

I used experimental parameters from Siegel (1986) to run the proposed model in different conditions of the task. First, the free parameters of the model were tuned in a way that the results of the model matched the experimental results in only one condition; and then, the free parameters were kept the same for the rest of the conditions. In general, the results of the model were similar to the experimental results. I believe that this similarity between the results of the model and experimental studies can serve as a validation process for the specification of the model's parameters, but not for the structure of the model. In other words, the model itself is a general and widely accepted Bayesian learning framework that needs to be explored by using different parameters set in order to understand different conditions of temporal bisection. Indeed, any set of parameters that is used to specify the

model is a hypothesis about subjects' learning and decision processes. For example, if a researcher wants to test the hypothesis that "human participants have a higher decay rate as compared to animal subjects" could use different decay rates in the model to verify this hypothesis.

Limitations and Future Directions

The proposed model helps to reconcile discrepancy between the human and animal temporal bisection literatures, which have remained divorced for decades, and gives new insight into the modeling of temporal perception. However, it is possible that the ecological validity of this model remains limited, as it is a computational explanation for existing experimental data. In the future, this model should be verified and revised by using new experimental designs and data. This mutual relationship between modeling and experimenting in science is of great importance to the co-evolution of both techniques.

Specifically, although we ran a sensitivity analysis to verify how different learning rates as free parameters of the model could impact the output of the model, experimental data are essential to verify the validity of this impact. The position of this thesis is that the motivational differences between human and animal subjects is one of the main reasons for the split between human and animal literatures covering the temporal bisection procedure. Thus, I recommend future studies control for motivational differences at the experimental level, if feasible. However, controlling for motivational differences could be done at a statistical level by measuring the learning rate of the subjects in parallel experiments and using this measure to account for the difference in the location of the TIP between human and animal subjects. Future studies could also correlate individual learning rates and location of the TIP within an experiment to account for variance among

individuals.

Moreover, now that it is shown that the assumption about the distribution of temporal perception is a critical factor in understanding the location of the TIP and consequently the interpretation of temporal bisection results, experimentalists should try to find the exact shape of this distribution in order to obtain more accurate output from the model. Currently, a theoretical and positively skewed distribution is used in the model, obtained by using the scalar property of timing. Although this distribution may not be the real distribution of temporal perception, it is better than a normal distribution in terms of its agreement with experimental results and data.

The proposed model enjoys more structural flexibility rather than flexibility in free parameters. The components of structural flexibility within this model are: A) how the model learns and updates the perceptions of anchor durations, and B) how the model decides about durations; this provides researchers with a platform to answer their questions about time perception in a dynamic “learning-decision” framework. In other words, the learning and decision processes of the model need to be specified based on the task in order to understand how time is perceived by subjects. Thus, we recommend future studies to answer questions about learning and decision processes first, rather than finding a theory or model that fits to the experimental results by capturing maximum variance.

The discussed structural flexibilities of the model could be utilized to understand exceptional phenomena like “Response Reversal” in the temporal bisection procedure. For example, future studies might answer how presenting out-of-range durations in temporal bisection impact the learning or decision processes of the subjects and use the model to verify their results by changing learning and decision processes.

Additionally, other models and theories developed for different types of timing tasks could adopt the structure of this model in order to explain the temporal perception in a dynamic learning-decision platform. For example, Information Processing model of timing originally developed by Treisman (1963) could use single trial level learning in order to update the Reference Memory in every trial by using the error of the response in Fixed and Peak Interval task which originally described by Catania (1970); all coincidence detection models of timing such as Miall's model (Miall, 1989) and Striatal Beat Frequency model (Matell & Meck, 2004) could update the coincidence detection network even in the test trials in order to have a dynamic learning process.

Conclusion

Models, in general, could have different purposes. One might give us predictability in which the system is usually considered a black box (predictive models); one might give us a description of a system in which the attempt is to understand the system (descriptive models). For example, a straightforward linear model might predict individuals' income based on their education level with high accuracy, but will not help us to understand the underlying mechanism. Although, a reasonably complex model might give us low predictive accuracy in the beginning, it can improve our understanding of the system and could gain predictability power later by iterative refinement. Modeling in science, and in this case the temporal bisection procedure, usually departs from understanding the mechanism by trying to match the results of the model to the results of experiments rather than matching the structure of the model to the structure of mechanisms of behavior. In this thesis, I focus on the structure of the model rather than predicting the results and implemented a framework that gives flexibility to researchers in order to verify different

hypotheses. Perhaps not understanding the reasons for gaps between the human and animal literatures on temporal bisection has a root in the purpose of modeling in this field.

DATA AVAILABILITY AND REPRODUCIBLE RESULTS

The data and codes for the model and figures are available at the following GitHub repository: <https://github.com/qiisziilbash/Temporal-Bisection>. MATLAB 2019a was used to develop the model and generate the figures. For any questions about the codes, contact Mahdi Shafiei (@qiisziilbash) at GitHub.

REFERENCES

- Akdoğan, B., & Balçı, F. (2016). Stimulus probability effects on temporal bisection performance of mice (*Mus musculus*). *Animal cognition*, *19*(1), 15-30.
- Allan, L. G. (2002). The location and interpretation of the bisection point. *The Quarterly Journal of Experimental Psychology: Section B*, *55*(1), 43-60.
- Allan, L. G., & Gibbon, J. (1991). Human bisection at the geometric mean. *Learning and motivation*, *22*(1-2), 39-58.
- Brown, G. D., McCormack, T., Smith, M., & Stewart, N. (2005). Identification and bisection of temporal durations and tone frequencies: common models for temporal and non temporal stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(5), 919.
- Buhusi, C. V., & Cordes, S. (2011). Time and number: the privileged status of small values in the brain. *Frontiers in integrative neuroscience*, *5*, 67.
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature reviews neuroscience*, *6*(10), 755.
- de Castro, A. C. V., Machado, A., & Tomanari, G. Y. (2013). The context effect as interaction of temporal generalization gradients: Testing the fundamental assumptions of the Learning-to-Time model. *Behavioural processes*, *95*, 18-30.
- Catania, A. C. (1970). Reinforcement schedules and psychophysical judgment: A study of some temporal properties of behavior. *The theory of reinforcement schedules*.
- Church, R. M., & Deluty, M. Z. (1977). Bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behavior Processes*, *3*(3), 216.
- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of

- cognitive science. *Behavioral and brain sciences*, 36(3), 181-204.
- Cowles, J. T., & Finan, J. L. (1941). An improved method for establishing temporal discrimination in white rats. *The Journal of Psychology*, 11(2), 335-342.
- Droit-Volet, S., Meck, W. H., & Penney, T. B. (2007). Sensory modality and time perception in children and adults. *Behavioural processes*, 74(2), 244-250.
- Droit-Volet, S., & Wearden, J. H. (2001). Temporal bisection in children. *Journal of Experimental Child Psychology*, 80(2), 142-159.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological review*, 84(3), 279.
- Grossberg, S., & Schmajuk, N. A. (1989). Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Networks*, 2(2), 79-102.
- Jeffress, L. A. (1948). A place theory of sound localization. *Journal of comparative and physiological psychology*, 41(1), 35.
- Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological review*, 95(2), 274.
- Kopec, C. D., & Brody, C. D. (2010). Human performance on the temporal bisection task. *Brain and cognition*, 74(3), 262-272.
- Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: coincidence detection of oscillatory processes. *Cognitive brain research*, 21(2), 139-170.
- Miall, C. (1989). The storage of time intervals using oscillating neurons. *Neural Computation*, 1(3), 359-371.

- Mioni, G., Capizzi, M., Vallesi, A., Correa, Á., Di Giacopo, R., & Stablum, F. (2018). Dissociating explicit and implicit timing in Parkinson's disease patients: evidence from bisection and foreperiod tasks. *Frontiers in human neuroscience, 12*, 17.
- Oprisan, S. A., & Buhusi, C. V. (2011). Modeling pharmacological clock and memory patterns of interval timing in a striatal beat-frequency model with realistic, noisy neurons. *Frontiers in Integrative Neuroscience, 5*, 52.
- Platt, J. R., & Davis, E. R. (1983). Bisection of temporal intervals by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 9*(2), 160.
- Poling, A., Nickel, M., & Alling, K. (1990). Free birds aren't fat: Weight gain in captured wild pigeons maintained under laboratory conditions. *Journal of the Experimental Analysis of Behavior, 53*(3), 423-424.
- Raslear, T. G. (1985). Perceptual bias and response bias in temporal bisection. *Perception & Psychophysics, 38*(3), 261-268.
- Raslear, T. G. (1983). A test of the Pfanzagl bisection model in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 9*(1), 49.
- Raslear, T. G. (1975). THE EFFECTS OF VARYING THE DISTRIBUTION OF GENERALIZATION STIMULI WITHIN A CONSTANT RANGE UPON THE BISECTION OF A SOUND- INTENSITY INTERVAL BY RATS 1. *Journal of the experimental analysis of behavior, 23*(3), 369-375.
- Reynolds, G. S., & Catania, A. C. (1962). Temporal discrimination in pigeons. *Science, 135*(3500), 314-315.
- Siegel, S. F. (1986). A test of the similarity rule model of temporal bisection. *Learning and Motivation, 17*(1), 59-75.

- Staddon, J. E. R., & Higa, J. J. (1999). Time and memory: Towards a pacemaker- free theory of interval timing. *Journal of the experimental analysis of behavior*, 71(2), 215-251.
- Stubbs, A. (1968). THE DISCRIMINATION OF STIMULUS DURATION BY PIGEONS. *Journal of the experimental analysis of behavior*, 11(3), 223-238.
- Stubbs, D. A. (1976). RESPONSE BIAS AND THE DISCRIMINATION OF STIMULUS DURATION. *Journal of the Experimental Analysis of Behavior*, 25(2), 243-250.
- Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the " internal clock". *Psychological Monographs: General and Applied*, 77(13), 1.
- Wearden, J. H. (1991). Human performance on an analogue of an interval bisection task. *The Quarterly Journal of Experimental Psychology Section B*, 43(1b), 59-81.
- Wearden, J. H., & Ferrara, A. (1995). Stimulus spacing effects in temporal bisection by humans. *The Quarterly Journal of Experimental Psychology*, 48(4), 289-310.
- Wearden, J. H., & Ferrara, A. (1996). Stimulus range effects in temporal bisection by humans. *The Quarterly Journal of Experimental Psychology Section B*, 49(1b), 24-44.
- Wearden, J. H., & Rogers P. & Thomas, P. R. R. (1997). Temporal bisection in humans with longer stimulus durations. *The Quarterly Journal of Experimental Psychology: Section B*, 50(1), 79-94.