A TEMPORAL INFORMATION-THEORETIC MODEL OF SUBOPTIMAL CHOICE

by

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ABSTRACT

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Suboptimal choice represents a form of maladaptive decision-making in which pigeons sacrifice food in order to earn stimuli that predict food. The study of suboptimal choice has the potential to reveal insights into the manner in which food-predictive stimuli (or reward-predictive stimuli more generally) encourage maladaptive decisions that might bear relevance to problematic gambling in humans. However, rats do not engage in suboptimal choice under conditions in which pigeons do, thereby raising questions about the species-generality of suboptimal choice. Thus, if the study of suboptimal choice is to reveal meaningful insights into the influence of reward-predictive stimuli in clinically relevant maladaptive decision-making, it is important to clarify the conditions under which rats might engage in suboptimal choice. Chapter 2 proposes and describes the temporal information-theoretic model which provides a formal framework that can inform experiments on suboptimal choice in rats and provide well-defined concepts to interpret and understand potential differences in suboptimal choice between rats and pigeons. The model is based on the notion that suboptimal choice is governed by competition between the bits of temporal information conveyed by food-predictive stimuli and the rate of food delivery. Competition between these two sources of control depends on the delay to food relative to the delay to temporally informative stimuli at the choice point. Suboptimal choice occurs when temporal information outcompetes the relative rate of food delivery, which occurs when the delay to food is much longer than the delay to temporally informative stimuli. Chapter 3 describes an experiment showing that rats engaged in suboptimal choice when the delay to food was sufficiently long. Chapter 4 describes an experiment showing that suboptimal choice in rats did not decrease with longer delays to temporally informative stimuli. Results from these experiments suggest that competition between temporal information and the rate of food delivery in rats is governed solely by the delay to food at the choice point. Given limited data with pigeons suggesting that competition is based on the delay to *food relative to* the delay to temporally informative stimuli, it is possible that rats and pigeons differ in the variables that govern competition between temporal information and the rate of food delivery to determine choice. Overall, this project examines the processes that govern suboptimal choice in both rats and pigeons through 1) development of a quantitative model of suboptimal choice, and 2) experiments derived from model predictions to determine the variables that encourage suboptimal choice in rats.

(193 pages)

PUBLIC ABSTRACT

A Temporal Information-Theoretic Model of Suboptimal Choice

Paul J. Cunningham

Humans and animals often make decisions not in their long-term best interest. In one example, called suboptimal choice, pigeons sacrifice food for food-predictive stimuli. The study of suboptimal choice can reveal insights into the role of reward-predictive stimuli in maladaptive decision-making that characterizes numerous behavioral disorders. However, there is currently little evidence that rats engage in suboptimal choice, thereby raising questions about the species-generality of suboptimal choice. According to the temporal information-theoretic model, developed in Chapter 2, suboptimal choice emerges when pigeons pay more attention to the bits of temporal information conveyed by food-predictive stimuli than the rate of food delivery while making decisions. When there is a long delay to food, more attention is paid to food-predictive stimuli and suboptimal choice emerges in pigeons. Chapter 3 found that rats also engaged in suboptimal choice provided a sufficiently long delay to food. Further, when there is also a long delay to food-predictive stimuli, more attention is paid to the rate of food delivery and optimal choice emerges in pigeons. Chapter 4 found that suboptimal choice in rats was unaffected by delays to food-predictive stimuli. Thus, the processes that govern suboptimal choice are well-described by the temporal information-theoretic model of suboptimal choice for both rats and pigeons, though there might be species-differences in the variables that govern attention to food-predictive stimuli and food itself.

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C’mon you Blues!

Paul J. Cunningham

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CHAPTER I

INTRODUCTION

Maladaptive decision-making can be broadly defined as an objective decrease in some commodity or resource resulting directly from the pattern of choices made by an individual. For example, a foraging animal who regularly prefers locations offering less food than known, alternative locations would be making a “maladaptive decision”. Further, the human gambler who continues to spend money on slot machines despite losing money in the long run for doing so would also be making a “maladaptive decision”. The literature on decision-making is rife with examples of animals making decisions that are not in their long-term best interest (Fantino, 2012; Igaki, Romanowhich, & Sakagami, 2019; Zentall, 2014; 2019). These examples are perplexing when considered within the context of optimal decision-making mechanisms sculpted by natural selection (Stephens & Krebs, 1986) and the numerous theories of decision-making asserting that animals prefer more profitable options (e.g., Davison & McCarthy, 1988; Rangel, Camerer, & Montague, 2008). In this way, the study of maladaptive decision-making can provide novel insights into the kinds of information animals use to make decisions that are not readily apparent when decision-making is viewed from a normative perspective.

One form of maladaptive decision-making finds pigeons choosing an option that offers a relatively low probability of food in lieu of an alternative offering a higher probability of food. Specifically, pigeons are given a choice between two options that deliver probabilistic food following a delay (e.g., food is probabilistically delivered 10 s after a choice response for either alternative). One alternative, the "suboptimal" alternative, offers a relatively low probability of food (e.g., probability of food = 0.2) while the other, "optimal", alternative offers a relatively high probability of food (e.g., probability of food = 0.5). Importantly, the delay that bridges the gap between a choice response and probabilistic food includes stimuli that differentially signal food delivery for the suboptimal alternative but not the optimal alternative. Thus, the suboptimal alternative provides a low probability of food *with* stimuli that predict food whereas the optimal alternative provides a high probability of food but *without* food-predictive stimuli. When given this choice, pigeons prefer the suboptimal alternative. This pattern of choice results in a lower rate of food delivery than is possible in the decision-making context and is therefore referred to as suboptimal choice (for reviews, see Cunningham & Shahan, 2018; McDevitt et al., 2016; Zentall, 2016).

Decades of research has illustrated the fact that suboptimal choice is driven by the opportunity to earn informative, food-predictive stimuli. Pigeons prefer the suboptimal alternative only when it, but not the optimal alternative, provides stimuli that predict food (e.g., Gipson et al., 2009; Kendall, 1974; Zentall & Stagner, 2010). In this way, pigeons are willing to sacrifice food for stimuli that predict (provide information about) food. Thus, the study of suboptimal choice in pigeons has the potential to reveal the processes by which food-predictive stimuli, or reward-predictive stimuli more generally, influence various forms of maladaptive decision-making. Further, some have suggested that the processes that govern suboptimal choice in pigeons bear relevance to the processes that govern certain features of problematic gambling in humans (Zentall, 2014). It is argued that the stimulus-array accompanying a winning pull on a slot machine (i.e., reward-predictive stimuli) encourages individuals to continue gambling even though they lose money in the long run for doing so, much like pigeons continue choosing an alternative that offers food-predictive stimuli even though they earn less food overall for doing so (Molet et al., 2012). Thus, the study of suboptimal choice has the potential to reveal the influence of reward-predictive stimuli on decision-making processes that contribute to clinically relevant problem behavior.

However, the potentially far-reaching implications of suboptimal choice for understanding clinically relevant, maladaptive decision-making hit a roadblock when it was discovered that rats do not engage in suboptimal choice under conditions identical to those in which pigeons do (Alba et al., 2018; Lopez, Alba, & Orduña, 2018; Martinez et al., 2017; Ojeda, Murphy, & Kacelnik, 2018; Trujano & Orduña, 2016; Trujano, López, Rojas-Leguizamón, & Orduña, 2016). The finding that rats do not engage in suboptimal choice raised questions about the species-generality of the phenomenon. If suboptimal choice reflects a peculiarity in pigeon decision-making processes, what general conclusions can we draw from studying suboptimal choice about the manner in which reward-predictive stimuli influence maladaptive decision-making in the animal kingdom as a whole? Further, what relevance is the study of suboptimal choice to human decision-making processes that contribute to maladaptive gambling if rats, the gold-standard animal model for studying clinically relevant decision-making processes, do not engage in suboptimal choice? If suboptimal choice is indeed a pigeon-specific phenomenon, then its utility as a method for studying the influence of reward-predictive stimuli on clinically relevant forms of maladaptive decision making is severely limited. Thus, addressing potential differences and similarities in suboptimal choice between pigeons and rats has been a focal point of recent suboptimal choice research (Zentall, Smith, & Beckmann, 2019).

The purpose of this project is to develop a quantitative model of suboptimal choice in pigeons and use this model to explore the conditions in which rats might engage in suboptimal choice. Chapter 2 describes a quantitative model of suboptimal choice proposed by Cunningham & Shahan (2018). According to their "temporal information-theoretic" model, suboptimal choice is governed by the competing influence of the relative temporal information conveyed by food-predictive stimuli (i.e., the information they convey about *when* to expect food) and the relative rate of food delivery between suboptimal and optimal alternatives. Suboptimal choice emerges when temporal information outcompetes the rate of food delivery as a determinant of choice. Competition between these two sources of control is formalized with a weighting mechanism that depends on the ratio of the delay to food (D_f) and the delay to food-predictive stimuli (D_s) at the choice point (i.e., D_f/D_s). The weighting mechanism is governed by D_f/D_s based on data with pigeons suggesting that temporal information outcompetes the rate of food delivery with long delays to food (D_f) but not with long delays to food-predictive stimuli (D_s). Cunningham & Shahan (2018) showed that this model provides an accurate account of the vast majority of suboptimal choice data in pigeons. Thus, the temporal information-theoretic framework can inform experiments exploring suboptimal choice in rats while providing well-defined, quantitative concepts that can be used to understand differences and similarities in the processes that govern suboptimal choice between rats and pigeons.

The overarching goal of the experiments described in Chapters 3 and 4 was to use the temporal information-theoretic model to further clarify similarities and differences in the decision-making processes that govern suboptimal choice in rats and pigeons. These experiments focused on the weighting mechanism that governs competition between temporal information and the rate of food delivery as a determinant of choice. While there is evidence suggesting that competition is based on an interaction between the delay to food (D_f) and the delay to temporally informative stimuli (D_s) in pigeons, there are currently no experiments assessing the influence of these variables on suboptimal choice with rats. Thus, the experiments described in Chapters 3 and 4 sought to clarify the variables that govern competition between temporal information and the rate of food delivery in rats based on the variables that appear to govern competition in pigeons.

Chapter 3 describes an experiment on suboptimal choice in rats exploring the possibility that rats engage in suboptimal choice when the delay to food at the choice point is sufficiently long. Indeed, numerous experiments with pigeons suggest that longer delays to food increase suboptimal choice (e.g., Dunn & Spetch, 1990; Spetch, Belke, Barnet, Dunn, & Pierce, 1990; Spetch, Mondloch, Belke, & Dunn, 1994). The temporal information-theoretic model accounts for this finding with the assumption that increasing the delay to food at the choice point increases the influence of the relative temporal information conveyed by food-predictive stimuli on choice, resulting in preference for the suboptimal alternative. It is possible that previous failures to find suboptimal choice in rats were related to the fact that previous experiments did not provide rats with a sufficiently long delay to food. Results from the experiment described in Chapter 3 suggest that rats will indeed engage in suboptimal choice provided a sufficiently long delay to food.

According to the temporal information-theoretic model, the influence of relative temporal information as a determinant of choice does not depend solely on the delay to food at the choice point, but on the delay to food *relative to the delay to temporally informative stimuli* at the choice point. This feature of the model is based on limited and inconsistent evidence suggesting that increasing the delay to food at the choice point does not increase suboptimal choice when the delay to temporally informative stimuli is also relatively long (Dunn & Spetch, 1990; Zentall, Andrews, & Case, 2017). In other words, suboptimal choice occurs only if the delay to food at the choice point is relatively long *and* the delay to temporally informative stimuli at the choice point is relatively short. Chapter 4 describes an experiment assessing the possibility that longer delays to temporally informative stimuli reduce suboptimal choice in rats. Results from the experiment described in Chapter 4 suggest that longer delays to temporally informative stimuli do not decrease suboptimal choice in rats.

Overall, results from the experiments described in Chapters 3 and 4 suggest that competition between temporal information and the rate of food delivery is governed only by the delay to food in rats, rather than the delay to food *relative to* the delay to temporally informative stimuli. Chapter 5 summarizes experiments reported in Chapters 3 and 4 and their relevance to the temporal information-theoretic model in particular and maladaptive decision-making in general. Avenues for future research on suboptimal choice in rats are also discussed in Chapter 5.

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CHAPTER 2

Suboptimal Choice, Reward-Predictive Signals, and Temporal Information[1]

Abstract

Suboptimal choice refers to preference for an alternative offering a low probability of food (suboptimal alternative) over an alternative offering a higher probability of food (optimal alternative). Numerous studies have found that stimuli signaling probabilistic food play a critical role in the development and maintenance of suboptimal choice. However, there is still much debate about how to characterize how these stimuli influence suboptimal choice. There is substantial evidence that the temporal information conveyed by a food-predictive signal governs its function as both a Pavlovian conditioned stimulus and as an instrumental conditioned reinforcer. Thus, we explore the possibility that food-predictive signals influence suboptimal choice via the temporal information they convey. Application of this temporal information-theoretic approach to suboptimal choice provides a formal, quantitative framework that describes how food-predictive signals influence suboptimal choice in a manner consistent with related phenomena in Pavlovian conditioning and conditioned reinforcement. Our reanalysis of previous data on suboptimal choice in pigeons suggests that, generally speaking, preference in the suboptimal choice procedure tracks relative temporal information conveyed by food-predictive signals for the suboptimal and optimal alternatives. The model suggests that

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suboptimal choice develops when the food-predictive signal for the suboptimal alternative conveys more temporal information than that for the optimal alternative. Finally, incorporating a role for competition between temporal information provided by food-predictive signals and relative primary reinforcement rate provides a reasonable account of existing data on suboptimal choice.

Key Words: Suboptimal Choice, Temporal Information, Conditioned Reinforcement, Pavlovian Conditioning, Information Theory

Introduction

When presented with a choice between two alternatives offering delayed food with a relatively high versus a low probability, organisms (e.g., pigeons, starlings, humans) sometimes prefer the alternative associated with the lower probability of reinforcement (see McDevitt, Dunn, Spetch, & Ludwig, 2016; Zentall, 2016 for reviews). Preference for the low-probability alternative is deemed a "suboptimal" choice because it results in less reinforcement (e.g., food) overall than if the high-probability alternative was chosen exclusively. Suboptimal choice has recently received considerable empirical attention because the phenomenon may have a number of theoretical and practical implications.

First, suboptimal choice is puzzling from an optimal foraging perspective (Stephens & Kreb, 1986) because such choices fail to maximize the rate of food intake possible in the environment. This deviation from optimality has led to considerations about how selection pressures have shaped decision-making processes that, while adaptive under natural foraging situations, might be less so in constrained laboratory situations (e.g., Vasconcelos, Monteiro, & Kacelnik, 2015). In this sense, suboptimal choice has encouraged the incorporation of evolutionary perspectives in the study of maladaptive decision making in animals. Second, suboptimal choice is inconsistent with mechanistic or descriptive models of choice which suggest that animals direct relatively more behavior towards alternatives that provide relatively more reinforcement, such as the matching law (Herrnstein, 1961). In this sense, suboptimal choice might serve as a catalyst in developing and improving models that describe choice between sources of reinforcement. Finally, suboptimal choice has been viewed as an analogue to human gambling and has therefore received attention as a possible method for revealing basic behavioral processes involved in problematic gambling (Zentall, 2014).

Although there is still much to be learned about suboptimal choice, research conducted thus far strongly suggests that stimuli predicting the outcome of a choice response play a critical role in the development and maintenance of suboptimal choice. Specifically, suboptimal choice emerges only when choice for the low-probability, suboptimal alternative produces stimuli differentially signaling whether or not food will be delivered for that response (see McDevitt et al., 2016 and Zentall, 2016 for reviews). Thus, a thorough characterization of how such stimuli influence choice is a critical first step in understanding suboptimal choice.

Many have argued that food-predictive stimuli in the suboptimal choice procedure have a disproportionate impact on choice because they provide information about the availability of food and/or because they serve as conditioned reinforcers (e.g., Iigaya et al., 2017; McDevitt et al., 2016; Zentall, 2016; Vasconcelos et al., 2015). The challenge for explaining suboptimal choice in terms of conditioned reinforcement is to not only identify how these stimuli function as conditioned reinforcers, but also why the conditioned reinforcer for the suboptimal alternative would be favored over one for the optimal alternative. Further, although information provided by food-predictive stimuli is often invoked in discussions of suboptimal choice (e.g., Vasconcelos et al., 2015; Fortes, Vasconcelos, & Machado, 2016; Fortes, Machado, & Vasconcelos, 2017), exactly what it means for these stimuli to provide information is never formalized. Nevertheless, it has long been suspected that the ability of a stimulus to function as a conditioned reinforcer might be related to the information the stimulus conveys about primary reinforcement.

However, early attempts to formalize this relation between conditioned reinforcement and information (e.g., Hendry, 1969) were abandoned because formal characterizations of the information about *whether or not* a stimulus would be followed by food failed to adequately address data from common procedures used to study conditioned reinforcement (see Fantino, 1977; Shahan & Cunningham, 2015, for reviews).

In order to address the previous shortcomings of an information-based approach to conditioned reinforcement, Shahan and Cunningham (2015) applied a more recent information-theoretic account of Pavlovian conditioning (see Balsam, Drew, & Gallistel, 2010; Gallistel & Balsam, 2009) to instrumental conditioned reinforcement. Specifically, based on this account, Shahan and Cunningham suggested that conditioned reinforcers acquire their ability to attract and maintain behavior as a result of the *temporal* information they convey about food (i.e., information about *when* to expect food). As we will discuss below, Shahan & Cunningham showed that such a temporal information-theoretic approach can provide a viable account of how food-predictive signals control behavior in preparations commonly used to study conditioned reinforcement (e.g., observing-response procedure, concurrent-chains). Thus, this temporal information theoretic approach provides an alternative to the numerous other theories of conditioned reinforcement developed within the context of concurrent-chains procedures (e.g., Delay-Reduction Theory, Fantino, 1977; Contextual Choice Model, Grace, 1994; Hyperbolic Value-Added Model, Mazur, 2001; Incentive Theory, Killeen, 1982). Unlike these other theories of conditioned reinforcement, the temporal information-theoretic approach directly formalizes the intuition that information and conditioned reinforcement are intimately related. Further, because the same basic framework is used for Pavlovian conditioning (e.g., Balsam et al., 2010), the temporal information-theoretic approach provides a quantitative basis for integrating Pavlovian conditioning and instrumental conditioned reinforcement--two domains long thought to be governed by the same processes (e.g., Mackintosh, 1974; Staddon, 1983; Williams, 1994).

Given the critical role of food-predictive signals in suboptimal choice, the temporal information-theoretic approach to conditioned reinforcement might also provide a useful framework to understand how these signals influence suboptimal choice. Specifically, food-predictive signals might influence suboptimal choice as a result of the temporal information they convey. Thus, the purpose of this paper is to extend the temporal information-theoretic approach to suboptimal choice. First, we present a brief review of existing accounts of how food-predictive signals influence suboptimal choice. Second, we describe the temporal information-theoretic approach to Pavlovian conditioning and its extension to instrumental conditioned reinforcement. Third, we describe how to calculate the temporal information conveyed by stimuli that follow choice responses in the suboptimal choice procedure. Fourth, we reanalyze existing data on suboptimal choice to assess the degree to which suboptimal choice depends on the relative temporal information conveyed by stimuli for suboptimal and optimal alternatives. Finally, as a first approximation to a working quantitative model of suboptimal choice based on temporal information, we consider how temporal information and primary reinforcement rate might compete to determine choice.

Conditioned Reinforcement and Suboptimal Choice

Early research on suboptimal choice used a concurrent-chains procedure with pigeons to assess choice between a low probability versus a high probability of reinforcement. Specifically, responding in the initial-link (IL) intermittently provided access to the terminal-link (TL) that ended in either food or blackout. For the suboptimal alternative, completion of the IL-TL chain resulted in a relatively low chance of food (often 50%). For the optimal alternative, completion of the chain resulted in food 100% of the time (e.g., Dunn & Spetch, 1990; Fantino, Dunn, & Meck, 1979; Kendall, 1974; 1985; Spetch et al., 1990). Although there were hints of suboptimal choice in this early research, there was often considerable between-subject and between-experiment variability in the degree of suboptimal choice (Mazur, 1996; Smith & Zentall, 2016; Zentall, 2016). Indeed, the first report of suboptimal choice by Kendall (1974) was questioned because of the unusual stimulus conditions used during the IL and TL (i.e., dark keys were used for IL stimuli and for the inoperative TL key). Fantino et al., (1979) subsequently failed to find suboptimal choice when these procedural details were corrected. However, Kendall (1985) again found suboptimal choice without the procedural details that plagued his first study. It is still not entirely clear why Kendall (1974; 1985) and Fantino et al., (1979) found discrepant results. Further, early research on suboptimal choice often found, at most, indifference between suboptimal and optimal alternatives, rather than preference for the suboptimal alternative (e.g., Dunn & Spetch, 1990; Fantino et al., 1979; McDevitt et al., 1997; Spetch et al., 1990; Spetch et al., 1994). Although indifference between suboptimal and optimal alternatives is still suboptimal in the sense that it reduces the overall rate of reinforcement, it is not quite as powerful a demonstration of suboptimal choice as that obtained in more recent research on suboptimal choice (to be discussed below). Thus, the inconsistent results from Kendall's and Fantino and colleagues' experiments, along with the fact that pigeons only rarely preferred the suboptimal alternative, illustrates the difficulties with clearly interpreting early research on suboptimal choice.

Gipson, Alessandri, Miller, and Zentall (2009) were arguably the first to find a relatively strong preference for the suboptimal alternative consistently across pigeons. Unlike most of the earlier research on suboptimal choice, Gipson et al., (2009) used a discrete-trial choice procedure (see Figure 1) in which a single response in the choice phase (i.e., a fixed ratio 1 IL schedule) initiated a delay (i.e., TL) that was accompanied by a stimulus change ending in food with probability, *p,* or blackout with probability, 1 - *p*. Each choice trial was separated by an inter-trial interval (ITI) during which the chamber was dark and response keys were inoperative. Choice for the suboptimal alternative ended in food with a relatively low probability whereas choice for the optimal alternative ended in food with a relatively high probability. All suboptimal choice

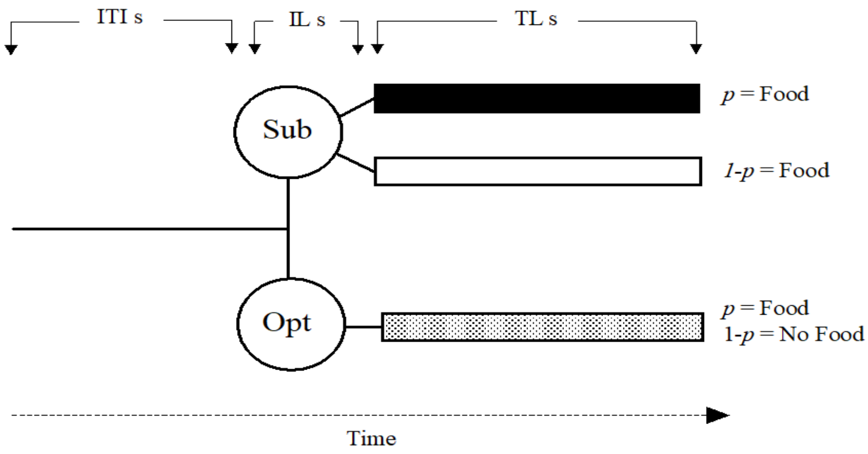

Figure 1. A depiction of the discrete-trial choice procedure used to study suboptimal choice. For simplicity we have shown only one terminal-link (TL) stimulus for the optimal alternative. However, research typically uses two stimuli that signal the same delay to and probability of reinforcement. As long as a color bias is not present, the use of one or two stimuli for the optimal alternative is inconsequential.

research conducted since Gipson et al., (2009) has used a discrete-trial choice procedure that is structurally similar to the one just described.

A critical variable in this procedure influencing suboptimal choice is whether TL stimuli following a choice response differentially signal the outcome for that response (i.e., food or no food). Specifically, pigeons more frequently choose the suboptimal alternative only when probabilistic food for that alternative is differentially signaled by a distinct TL stimulus (e.g., a choice response to the suboptimal alternative is followed by a blue light when food will be delivered and a red light when food will not be delivered). When TL stimuli do not differentially signal the outcome for a suboptimal choice response (e.g., a choice response to the suboptimal alternative is followed by a yellow light both when food is and is not delivered), pigeons prefer the optimal alternative. The critical role of TL stimuli differentially signaling choice outcomes in suboptimal choice has been demonstrated numerous times and across a variety of procedural parameters (see McDevitt et al., 2016 and Zentall, 2016 for reviews).

Although the evidence is clear that TL stimuli differentially signaling choice outcomes play a critical role in suboptimal choice, there is still no consensus about how to characterize the impact of these TL stimuli on choice. Perhaps the most widely accepted view is that the TL stimulus signaling food for the suboptimal alternative serves as a conditioned reinforcer that supports choice responses for that alternative. In this sense, in order to understand suboptimal choice, it is necessary to characterize how TL stimuli function as conditioned reinforcers in a way that can explain why the TL stimulus for the suboptimal alternative is preferred to TL stimulus for the optimal alternative.

Because the suboptimal choice procedure is a variant of the concurrent-chains procedure, it is possible that any one of the many existing theories of concurrent chains performance (e.g., Delay Reduction Theory, Contextual Choice Model, etc.) might be extended and/or modified to account for suboptimal choice. Nevertheless, with the exception of Delay Reduction Theory (see SiGN Hypothesis below), such models have not been extended to suboptimal choice, and doing so is beyond the scope of this paper. Rather, for the reasons described in the Introduction section above (and explored further later), we prefer a temporal information-theoretic approach to conditioned reinforcement and will thus focus our developmental efforts on extending such an approach to suboptimal choice. But first, we shall briefly review existing theories explicitly aimed at explaining suboptimal choice.

The SiGN Hypothesis. The Signals for Good News hypothesis of suboptimal choice (SiGN hypothesis; Dunn & Spetch, 1990; McDevitt et al., 2016) is based in part on Delay Reduction Theory, which states that the value of a conditioned reinforcer depends on the reduction in delay to food signaled by a stimulus relative to the overall average delay to food (Fantino, 1977). The SiGN hypothesis argues that TL stimuli in the suboptimal choice procedure serve as conditioned reinforcers to the extent that they signal a reduction in delay to food *relative to the choice response itself*. Thus, the SiGN hypothesis differs from DRT in that delay reduction is assessed relative to the choice response in the SiGN hypothesis, but in DRT is assessed relative to the overall delay to food. Further, it is assumed that a stimulus that does not signal food has no effect on choice. To see how this works, consider a choice between a suboptimal alternative offering a 50% chance of food, with TL stimuli that differentially signal food and no food, and an optimal alternative offering food 100% of the time. Probabilistic food for the suboptimal alternative and TL stimuli that differentially signal the presence and absence of food create a context in which the food-predictive TL stimulus for that alternative results in a greater reduction in delay to food than the choice response itself (because the choice response is followed by food 50% of the time whereas the food-predictive signal is followed by food 100% of the time). However, because a choice response to the optimal alternative is always followed by food, the TL stimulus for that alternative is not associated with a reduction in delay to food beyond the reduction produced by the choice response itself. Thus, the food-predictive TL stimulus for the suboptimal alternative serves as a stronger conditioned reinforcer than the TL stimulus for the optimal alternative, resulting in preference for the suboptimal alternative. It is important to note that the SiGN hypothesis informally suggests a role for the direct effects of delayed primary reinforcement in suboptimal choice, though details of the interaction between delayed primary reinforcement and immediate conditioned reinforcement remain unspecified within the account.

McDevitt et al., (2016) provide a review of how the SiGN hypothesis might account for a variety of data on suboptimal choice in pigeons and suggest that it provides a viable conceptual framework for understanding suboptimal choice. However, there are a couple of important conceptual issues worth noting with the SiGN hypothesis. First, the SiGN hypothesis is at present only a broad conceptual framework that does not offer any formal, quantitative definitions of 1) how to calculate delay reduction relative to a choice response under the variety of conditions to which it has been applied, 2) how to quantify the impact of primary reinforcement on choice, and 3) how conditioned and primary reinforcement interact to determine choice. A more thorough analysis of the SiGN hypothesis, and its ability to provide an accurate quantitative description of suboptimal choice, must await its formal development. Second, the generality of the definition of conditioned-reinforcer value according to the SiGN hypothesis is not clear. For example, DRT defines conditioned-reinforcer value in a way that can capture its effect on behavior across a range of procedures used to study conditioned reinforcement, such as the concurrent-chains procedure and the observing-response procedure (see Fantino 1977 for review). Although the SiGN hypothesis is based on DRT, the change in reference point for assessing delay reduction (i.e., relative to the choice response in the SiGN hypothesis versus relative to the overall average delay to food in DRT) drastically changes what it means for a stimulus to serve as a conditioned reinforcer. At the moment, it is not clear if the definition of conditioned-reinforcer value proposed by the SiGN hypothesis can accurately characterize conditioned reinforcement in general, or if its definition is restricted to the suboptimal choice procedure.

The Predictive Value Hypothesis. An alternative approach to suboptimal choice offered by Zentall and colleagues suggests that choice depends solely on the predictive value of conditioned reinforcers that follow a choice response, where predictive value is defined as the probability and amount of food signaled by a TL stimulus (Zentall, 2016). Much like the SiGN hypothesis, the predictive value hypothesis assumes that a stimulus that does not signal food has no effect on choice. From this perspective, suboptimal choice emerges when the TL stimulus for the suboptimal alternative is associated with a higher probability or greater amount of food than that for the optimal alternative. For example, Gipson et al., (2009) assessed choice between a suboptimal alternative offering food 50% of the time (with differential stimuli signaling food and no food) and an optimal alternative offering food 75% of the time (without differential stimuli signaling food and no food). Importantly, the probability of food delivery signaled by the food-predictive TL stimulus for the suboptimal alternative (i.e., $p = 1$) was greater than that for the optimal TL stimulus (i.e., $p = .75$). Under these conditions, the predictive value hypothesis expects preference for the suboptimal alternative because the TL stimulus for that alternative had more predictive value (i.e., it was associated with a higher probability of food delivery), and indeed preference favored the suboptimal alternative under these conditions. Stagner & Zentall (2010) subsequently found even stronger preference for the suboptimal alternative when the probability of food delivery signaled by the optimal TL stimulus was 0.5 while the suboptimal food-predictive TL stimulus signaled food with a probability of 1 (i.e., an even greater difference in the probability of food delivery signaled by suboptimal and optimal TL stimuli than in Gipson et al., 2009). Further, Zentall & Stagner, (2011a) examined choice between a suboptimal alternative offering 10 food pellets 20% of the time (with differential stimuli signaling food and no food) and an optimal alternative offering 3 food pellets 100% of the time. Although the TL stimuli for both alternatives signaled food with a probability of 1, the TL stimulus for the suboptimal alternative signaled a greater amount of food. As expected by the predictive value hypothesis, preference for the suboptimal alternative developed. Thus, this perspective argues that suboptimal choice is governed by the conditioned-reinforcing value of TL stimuli, and that the conditioned-reinforcing value of a TL stimulus depends on its predictive value.

Although this approach might provide a reasonable heuristic for identifying the conditions under which suboptimal choice develops, it cannot provide a general account of how stimuli serve as conditioned reinforcers. Indeed, characterizing the value of a conditioned reinforcer in terms of its associated probability of food delivery and the amount of food it signals is too narrow a characterization to capture the wide variety of variables known to influence conditioned-reinforcer value, perhaps most important of which are temporal variables. Thus, this approach, at least in its current form, cannot provide an account of how stimuli serve as conditioned reinforcers in a manner that can integrate their role in suboptimal choice into the larger framework of conditioned reinforcement in general. For this reason, the predictive-value hypothesis is limited.

The Ecological Model. Unlike the accounts of suboptimal choice just described, the ecological model does not suggest that TL stimuli influence suboptimal choice through their conditioned-reinforcing value *per se*. Rather, this approach suggests that suboptimal choice reflects an information-seeking strategy that has evolved because of its adaptive effects in natural foraging situations, but can result in maladaptive effects under contrived laboratory settings (Fortes et al., 2017; Vasconcelos et al., 2015). Specifically, it is argued that when animals forage for food, signals that convey information about whether or not food is available provide an adaptive benefit by allowing abandonment of a foraging option that will not lead to food. In other words, when animals receive a signal that tells them food is not forthcoming (i.e., an S-), the animal can abandon that foraging option and pursue food elsewhere, thereby avoiding the opportunity costs of waiting for food that is not available. This adaptive benefit in natural foraging situations set the stage for natural selection to favor decision-making strategies that consider informative signals in decisions about which foraging options to pursue. This decision-making strategy therefore favors the suboptimal alternative when it, but not the optimal alternative, provides informative TL stimuli (i.e., TL stimuli that differentially signal choice outcomes). However, this evolved strategy (i.e., pursing foraging options that provide informative signals) backfires in the suboptimal choice procedure because the animal is forced to pay the opportunity cost of waiting for food that is not available, which it would not have to do in natural foraging situations. Thus, this perspective argues that suboptimal choice reflects an evolved preference for foraging options that provide information about the presence or absence of food.

The ecological model of suboptimal choice formalizes this notion using models of energy-intake rate (i.e., energy gained from food / time spent searching for food) from Optimal Foraging Theory (Stephens & Krebs, 1986). Broadly speaking, when the suboptimal alternative provides informative TL stimuli, all delays associated with trials in which food is not delivered (e.g., notably time spent in the S-) are not included in energy-intake rate calculations for that alternative, much like an animal foraging in the wild would not incur the opportunity costs of waiting for food they know is not available. Removing these delays from energy-intake rate for the suboptimal alternative increases the functional rate of energy intake for that alternative. Because the optimal alternative does not provide informative TL stimuli (i.e., there is no S-), delays associated with trials in which food is not delivered are included in calculations of energy-intake rate for that alternative, much like an animal foraging for food without informative signals would incur these opportunity costs. Preference for the suboptimal alternative is therefore expected because the *functional* rate of energy intake for that alternative is actually higher than that for the optimal alternative once energy-intake rate calculations have been adjusted based on the presence or absence of informative stimuli for each alternative.

It is important to note that the ecological model of suboptimal choice is meant primarily as a means to understand how natural selection might shape decision-making strategies that are sensitive to information. Thus, like most evolutionary perspectives on behavior, the ecological model is meant primarily as a framework to understand the evolutionary origins of whatever behavioral process results in suboptimal choice (Fortes et al., 2016). However, its emphasis on information about whether or not food will occur at the evolutionary level seems to suggest that the behavioral processes responsible for suboptimal choice should also be sensitive to this kind of information. Nevertheless, an information-oriented approach like the one just described, whether focused on the phylogenetic or ontogenetic level, should offer a formal, quantitative definition of what it means for a stimulus to convey "information" about food. Indeed, a formal definition of information is especially important for the ecological model of suboptimal choice given that the presence or absence of informative stimuli serves as the basis for removing (or not) certain temporal intervals from energy-intake rate calculations. Without a formal definition of information, the rules for calculating energy-intake rate for a given choice alternative depend only on informal, subjective interpretations of what it means for an alternative to provide "informative" signals.

Although the ecological model of suboptimal choice has yet to provide a formal definition of what it means for TL stimuli to provide information about *whether or not* food will occur, such a formalization served as the basis of an information-theoretic approach to conditioned reinforcement developed over 50 years ago to explain observing behavior (i.e., Hendry, 1969). Observing behavior is defined as a response that produces discriminative stimuli signaling whether primary reinforcement is available (i.e., S+) or not (i.e., S-; Wycoff, 1952). Indeed, the suboptimal choice procedure is probably best understood as a variant of the observing response procedure because choice for the suboptimal alternative provides discriminative stimuli (i.e., the S+ and the S-) whereas choice for the optimal alternative does not (see Roper & Zentall, 1999). In essence, this arrangement has much in common with early E-maze based observing procedures used to study rats' preference for differentially signaled outcomes (i.e., rewarded versus unrewarded trials) versus non-differentially signaled outcomes (e.g., Prokasy, 1956). The information-theoretic approach to observing suggested that the ability of a discriminative stimulus to maintain observing depends on the amount of information it conveys about *whether or not* primary reinforcement is available, much like the ecological model of suboptimal choice implicitly suggests a critical role for "whether or not" information conveyed by TL stimuli in the suboptimal choice procedure. This information-theoretic approach to observing used Shannon information to quantify into bits how much information a discriminative stimulus conveys (Hendry, 1969),

$$H = \sum_i p_i \; log_2 \left(\frac{1}{p_i}\right), \tag{1}$$

where H refers to the average uncertainty (i.e., entropy) and p_i refers to the probability of the ith state among a set of possible states. When Equation 1 is applied to the observing-response procedure, the states refer to periods of primary reinforcement (i.e., S+) and extinction (i.e., S-). Thus, for a typical observing procedure (and for the suboptimal alternative in suboptimal choice procedures) where trials with and without food occur with p=.5 (i.e., pS+ = pS- = .5), a stimulus presentation can reduce uncertainty by one bit.

Generally speaking, this perspective argued that stimuli that convey information (i.e., reduce uncertainty) about whether or not primary reinforcement is available should serve as conditioned reinforcers, and that stimuli that convey more information should be more potent conditioned reinforcers.

Application of Equation 1 to conditioned reinforcement generated two testable predictions about the degree to which discriminative stimuli should maintain observing behavior. First, the stimulus that signals the absence of primary reinforcement (i.e., the S-) should be sufficient by itself to maintain observing because it conveys the same amount of information as the stimulus that signals the availability of primary reinforcement (e.g., 1 bit when pS+ = pS- =.5) in a typical observing procedure. Second, discriminative stimuli should be most effective at maintaining observing when trials with and without food occur with p=.5 (i.e., pS+ = pS- = .5) and should decrease in efficacy as a symmetrical inverted U-shaped function as availability of primary reinforcement approaches either 0 or 1. More thorough reviews of research assessing these predictions can be found elsewhere (e.g., Fantino, 1977; Shahan & Cunningham, 2015), but for present purposes it is sufficient to note that neither of these predictions were supported by the data. Thus, the notion that the conditioned-reinforcing value of discriminative stimuli is governed by the information they convey about *whether or not* primary reinforcement is available was abandoned. For this reason, characterizing the effect of TL stimuli on suboptimal choice in terms of the information they convey about whether or not food will occur, as the ecological model of suboptimal choice implies, is incompatible with the wealth of evidence on this issue in the observing literature. Indeed, Roper and Zentall (1999) also found that preference between alternatives that provided discriminative and non-discriminative TL stimuli was not consistent with predictions generated by Equation 1. For this reason, it seems counterintuitive to focus on how evolutionary pressures shape decision-making mechanisms that are designed to respond to sources of information (i.e., whether or not food will occur) that do not appear to influence animal decision-making in laboratory conditions very similar to those arranged by suboptimal choice procedures.

Despite the empirical failures of the information-theoretic approach described by Equation 1, there is still a widely held belief that food-predictive signals influence behavior because of the information they convey. As Shahan and Cunningham (2015) noted, the failure of Equation 1 to accurately characterize conditioned reinforcement does not require one to abandon an information-theoretic approach altogether. Rather, previous information-theoretic approaches to behavior maintained by food-predictive signals likely failed because formal application of information theory was directed at the wrong source of information. Recent conceptual developments in the Pavlovian conditioning literature have identified temporal information (i.e., information about *when* to expect food) as the critical source of information governing the impact of food-predictive signals on behavior within typical conditioning experiments. Based on the notion that Pavlovian conditioning governs how stimuli function as conditioned reinforcers, Shahan and Cunningham (2015) argued that temporal information might also govern the degree to which a food-predictive signal serves as a conditioned reinforcer. In the next section, we review the temporal information-theoretic approach to Pavlovian conditioning and its extension to conditioned reinforcement. This temporal information-theoretic approach might provide a quantitative framework to better formalize the notion that TL stimuli influence suboptimal choice through the information they convey.

Temporal Information, Pavlovian Conditioning, and Conditioned Reinforcement

The temporal information-theoretic approach to Pavlovian conditioning is based on the assertion that Pavlovian conditioning is defined by learning about the temporal distribution of events (e.g., food and arbitrary stimuli) in the environment, and that conditioned responding is supported by these learned temporal intervals (e.g., Gallistel & Gibbon, 2000). Given the critical role of timing in Pavlovian conditioning, the temporal information-theoretic approach suggests that a conditioned stimulus (CS) influences conditioned responding through the information it conveys about *when* to expect the next unconditioned stimulus (US; Balsam & Gallistel, 2009). Shannon entropy can be applied to the temporal distribution of USs in the presence and absence of a CS in order to quantify the degree to which a CS reduces uncertainty about when to expect a US. For simplicity, we assume that the intervals between USs and CSs are generated by a random-rate process, which results in an exponential probability distribution of inter-event intervals. There are three steps in calculating the temporal information conveyed by a CS. First, the average uncertainty about when to expect a US independent of any other event is calculated using the probability distribution of possible US-US intervals (i.e., cycle time, *C*). The entropy of an exponential distribution of possible US-US intervals is,

$$H_c = log_2 C + k \qquad (2),$$

where k is a constant ($e/\Delta\tau$) that depends on the animal's temporal resolution and transforms the continuous exponential distribution into discrete units with a width determined by $\Delta\tau$ (though k cancels out in the final equation). H_C represents the basal uncertainty about when to expect food in the experimental session, which sets an upper limit on how much information a signal can convey above and beyond the information conveyed by food delivery itself. Next, the average uncertainty about when to expect a US in the presence of the CS (i.e., H_t) is calculated using the probability distribution of possible CS-US intervals,

$$H_t = log_2 t + k \qquad (3),$$

where t refers to the average CS-US duration and k is as in Equation 2. H_t quantifies the uncertainty about when to expect food in the presence of the CS. Finally, temporal information conveyed by the CS (i.e., H) is measured by the degree to which onset of the CS reduces uncertainty about when to expect a US:

$$H = (log_2 C + k) - (log_2 t + k) \qquad (4),$$

which reduces to,

$$H = log_2(C/t) \qquad (5).$$

The temporal information-theoretic approach characterized by Equation 5 provides a means to formalize the long-standing intuition that a CS influences conditioned responding through the information it provides about the US (e.g., Rescorla, 1968). Indeed, the temporal information-theoretic approach characterized by Equation 5 can readily account for the phenomena that inspired researchers to think about Pavlovian conditioning in informational terms, such as Rescorla’s truly random control experiment and cue-competition effects such as blocking, overshadowing, and relative validity (see Balsam et al., 2010 for a review). Further, this temporal information-theoretic approach provides a principled reason for why the *C/t* ratio plays such a critical role in the acquisition of Pavlovian conditioned responding (Gallistel & Gibbon, 2000). Specifically, when a CS signals a greater reduction in delay to the US relative to the overall average delay to USs (i.e., a higher *C/t* ratio), that CS necessarily provides more temporal information about US delivery. As a result, conditioned responding emerges more quickly when a CS conveys more temporal information (Ward et al., 2012). Thus, the temporal information-theoretic approach defined by Equation 5 provides a means to quantify the information conveyed by a CS in a way that is consistent with a variety of Pavlovian phenomena.

Many have argued that the ability of a stimulus to serve as an instrumental conditioned reinforcer is governed by Pavlovian conditioning (e.g., Mackintosh, 1974; Staddon, 1983; Williams, 1994). If so, then Equation 5 might also govern the degree to which a stimulus serves as a conditioned reinforcer. The prospect of using information theory to characterize the conditioned-reinforcing value of a food-predictive signal stems from the belief that conditioned reinforcement is best understood as a guidance process (Bolles, 1975; Davison & Baum, 2006; Longstreth, 1971; Shahan, 2010; Staddon, 1983). According to this perspective, the reason animals respond for food-predictive signals is because they provide information about some relevant aspect of the world that is instrumental for finding food in space and time. In other words, responses that produce food-predictive signals are maintained by the feedback those signals provide about the state of the world that is relevant to the animal's motivation at that time (see also, Shahan, 2017). Such an approach implies a crucial role for the informational properties of a food-predictive signal, and information theory provides a quantitative framework to rigorously define (1) what it means for a stimulus to convey information, and (2) how much information a stimulus conveys. Application of information theory to the temporal parameters of a procedure suggests that animals are searching primarily for feedback about the timing of food deliveries. That is, time is the relevant environmental dimension that determines a signal's conditioned-reinforcing value in many procedures commonly used to study conditioned reinforcement.

Shahan and Cunningham (2015) pursued this notion by exploring the utility of Equation 5 for describing the degree to which animals respond for food-predictive signals in procedures commonly used to study conditioned reinforcement. First, Shahan and Cunningham calculated the temporal information conveyed by a stimulus predictive of primary reinforcement (i.e., S+) in a standard observing response procedure. Observing responses were found to increase as the temporal information conveyed by the stimulus predictive of primary reinforcement increased. Thus, temporal information appears to govern the degree to which food-predictive signals maintain observing behavior.

Second, Shahan and Cunningham explored the possibility that relative temporal informativeness (i.e., the information conveyed by food-predictive signals arranged for two separate alternatives, H_1 / H_2) might govern the impact of TL stimuli on choice in the standard concurrent-chains procedure. The extension of temporal information to concurrent-chains is of special importance because, as mentioned earlier, a large majority of formal theories of conditioned reinforcement value are based on choice in the concurrent-chains procedure. Thus, if the temporal information-theoretic approach can provide a viable account of conditioned reinforcement in general, it must also account for the role of conditioned reinforcement in the concurrent-chains procedure.

The three most ubiquitous findings in concurrent-chains research are (1) preference for a TL stimulus increases as the rate of reinforcement it signals increases relative to the rate of reinforcement signaled by the other TL stimulus, (2) preference for a TL associated with the relatively higher rate of reinforcement decreases as overall IL duration increases (i.e., the IL effect), and (3) preference for a TL associated with a relatively higher rate of reinforcement increases as overall TL duration increases (i.e., the TL effect). All viable models of concurrent-chains performance capture these three findings, and all of the concurrent-chains models mentioned above (e.g., Delay Reduction Theory, Contextual Choice Model, Hyperbolic Value Added model, Incentive Theory) make very similar predictions in this regard. Shahan & Cunningham (2015) showed that the temporal information-theoretic approach can capture these effects through variations in relative temporal informativeness (H_1 / H_2). Specifically, they showed that (1) the temporal information conveyed by a TL stimulus relative to the other increases as the rate of reinforcement it signals increases relative to the other, (2) a TL stimulus associated with a relatively higher rate of reinforcement becomes *less* temporally informative relative to the other TL stimulus as overall IL duration increases, and (3) a TL stimulus associated with a relatively higher rate of reinforcement becomes *more* temporally informative relative to the other TL stimulus as overall TL duration increases. In sum, the temporal information conveyed by a food-predictive signal can capture its effects on behavior in the most commonly-used procedures to study conditioned reinforcement (i.e., the observing response and concurrent-chains procedures).

Further, the temporal information-theoretic approach confers serval conceptual advantages over other theories of conditioned reinforcement. First, while all theories of conditioned reinforcement emphasize the role of temporal intervals in conditioned-reinforcer value (though in slightly different ways), only the temporal information-theoretic approach offers a principled reason for why temporal intervals are critical for conditioned reinforcement. To illustrate this point, consider Delay Reduction Theory (i.e., DRT), which states that the value of a stimulus as a conditioned reinforcer depends on the reduction in delay to food signaled by a stimulus (i.e., *t*) relative to the overall delay to food (i.e., *C*). DRT simply asserts that these temporal intervals determine the value of a stimulus as a conditioned reinforcer, but offers no principled reason for why that should be the case. However, the temporal information-theoretic approach provides a formal analytic reason why these temporal intervals (i.e., *C* and *t*) are critical. Namely, these are precisely the intervals required to calculate the temporal information conveyed by a food-predictive signal (see Equations 2-5). Indeed, Shahan & Cunningham (2015) noted that conditioned reinforcement value as calculated by DRT (see Fantino, 1981) provides a close (but not identical) approximation to the temporal information conveyed by food-predictive signals, and suggested that this approximation might be why DRT was a successful theory of conditioned reinforcement. Second, as noted above, the temporal information-theoretic approach offers a single, formal framework that unifies both Pavlovian conditioning and conditioned reinforcement. Thus, the temporal information-theoretic approach offers a parsimonious framework for describing how food-predictive signals impact behavior.

Given the critical role of food-predictive signals in suboptimal choice, and the success of the temporal information-theoretic approach in accounting for existing data on conditioned reinforcement, it is possible that the temporal information-theoretic approach can also provide a reasonable account of suboptimal choice. Perhaps organisms often prefer the suboptimal alternative because the food-predictive TL stimulus for that alternative conveys more temporal information than the non-predictive TL stimulus for the optimal alternative. An assessment of how suboptimal choice varies as a function of relative temporal informativeness conveyed by TL stimuli for suboptimal and optimal alternatives might clarify the role of temporal information in suboptimal choice. However, before this can be assessed, it is necessary to demonstrate how to calculate temporal information conveyed by TL stimuli in the suboptimal choice procedure.

Temporal Information in the Suboptimal Choice Procedure

We will use a discrete-trial suboptimal choice procedure, like the one depicted in Figure 1, with a 10 s inter-trial interval (ITI), a FR 1 IL schedules, and 10 s TL durations to demonstrate how to calculate the temporal information conveyed by TL stimuli for both suboptimal and optimal alternatives. These parameters were chosen because they are the most commonly used parameters in suboptimal choice research using a discrete-trial choice procedure. We will use only forced-exposure trials (i.e., trials in which only one alternative is presented on a given trial) to demonstrate how temporal information is calculated. We use forced-exposure trials because (1) a majority of trials in the suboptimal choice procedure are of this kind, (2) it is generally believed that choices in free-choice trials reflect what animals learn in forced-exposure trials, and (3) it does not require the incorporation of actual choices made by the animal in order to make the calculations, thereby simplifying calculations. The overall probability of food will be 0.2 for the suboptimal alternative and 0.5 for the optimal alternative. Importantly, probabilistic food delivered for the suboptimal and optimal alternatives can be either signaled or unsignaled by TL stimuli (see Figure 2). A choice alternative is “signaled” when distinct TL stimuli differentially signal whether or not food will be delivered for that choice response (i.e., when the probability of food following onset of the TL stimulus signaling food is 1.0; top panel of Figure 2). A choice alternative is “unsignaled” when TL stimuli do not differentially signal food delivery for that alternative (i.e., when the probability of food following onset of the TL stimulus is equal to the overall probability of food for that alternative; bottom panel of Figure 2).

It is important to emphasize that throughout this section we refer to only one TL stimulus for both suboptimal and optimal alternatives, even though suboptimal choice research often arranges two TL stimuli for each alternative. When an alternative provides TL stimuli that differentially signal food (i.e., a "signaled" alternative), we consider only the TL stimulus that signals food and ignore the S- (much like other approaches to suboptimal choice). Thus, there is only one TL stimulus associated with food for an alternative that is signaled, specifically the TL stimulus that signals each food delivery for that alternative. When an alternative does not provide TL stimuli that differentially signal food (i.e., an "unsignaled" alternative), each TL stimulus is associated with same probability of food delivery (e.g., each TL stimulus is followed by food with a probability of 0.5) and are therefore functionally equivalent. Thus, for simplicity we consider only

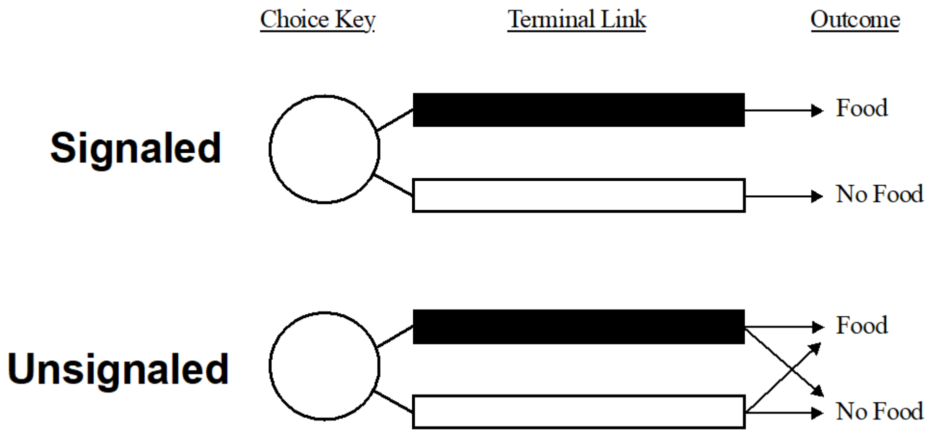

Figure 2. The top panel depicts the predictive relation between terminal-link stimuli and choice outcomes under signaled conditions. The bottom panel depicts the non-predictive relation between terminal-link stimuli and choice outcomes under unsignaled conditions (modified from McDevitt et al., 2016).

one of the TL stimuli for an unsignaled alternative, as considering both would be redundant.

Based on this description of the suboptimal choice procedure, there are four possible “signal conditions” that describe the relation between TL stimuli and choice outcomes for each alternative: (1) both suboptimal and optimal alternatives can be signaled, (2) both suboptimal and optimal alternatives can be unsignaled, (3) only the suboptimal alternative can be signaled, and (4) only the optimal alternative can be signaled. In order to calculate temporal information, it is necessary to first calculate the overall average time to food (i.e., cycle time, *C*), and second calculate the average time to food in the presence of a TL stimulus that is associated with food (i.e., trial time, *t*). Once *C* and *t* are calculated, we can explore how variations in the signaled relation between TL stimuli and choice outcomes, which is the variable that plays a critical role in suboptimal choice, influences temporal information conveyed by TL stimuli.

Cycle Time. In our example, each trial is separated by a 10 s ITI and the first response to a choice key after a latency of, say, 1 s (which is the IL duration in this example) produces either food or blackout after the 10 s TL. Thus, the inter-*outcome* interval is 10 s (ITI) + 1 s (IL) + 10 s (TL) = 21 s. The suboptimal alternative provides food with a probability of 0.2 whereas the optimal alternative provides food with a probability of 0.5. Forced-exposure trials ensure equal exposure to both alternatives (i.e., both the suboptimal and optimal alternatives are presented 50% of the time). Thus, the average expected time to food (i.e., *C*) is calculated as:

$$C = \frac{ITI\ s + IL\ s + TL\ s}{.5(pSr_{sub} + pSr_{opt})} \qquad (6),$$

where ITI, IL and TL durations are as defined above and *pSr* is the probability of food delivery for suboptimal or optimal alternative (denoted by the subscripts). For clarification, the numerator refers to the average expected time to an *outcome* whereas the denominator refers to the average probability that the outcome is food delivery[2]. In our example, then, $C = 21/ [.5(0.2+0.5)] = 60$ s. Note that *C* depends on the average number of trials until a food delivery, which is a geometrically distributed random variable with a mean that depends on the average probability of food for a trial outcome (i.e., the denominator of Equation 6). Thus, even though the suboptimal choice procedure often employs fixed-interval durations (e.g., ITI, TL, etc.), an exponential distribution of possible US-US intervals, as assumed by our calculations of entropy, provides a close approximation to what pigeons actually experience (the same is true for fixed CS-US durations that end probabilistically in food[3]).

It is important to emphasize that time spent in the presence of the stimulus that does not signal food (i.e., S-) also contributes to *C*. This is because it is necessary to include all temporal parameters of a procedure, regardless of their behavioral impact, in order to properly define basal temporal uncertainty. In other words, application of

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[2] In order to find obtained *C* in free-choice trials, simply weight pSr_{sub} by the proportion of suboptimal choices and pSr_{opt} by the proportion of optimal choices, rather than taking their unweighted average.

[3] However, the same is not true for fixed CS-US durations for TL stimuli that always end in food. A fixed CS-US duration adds an additional source of uncertainty based on the Gaussian distribution resulting from noise in the animal's timing processes (see Balsam et al., 2010 for description of how to calculate temporal uncertainty with fixed CS-US intervals). There is currently no evidence that this additional source of uncertainty influences the acquisition of conditioned responding (e.g., Ward et al., 2012) and might therefore be behaviorally irrelevant. Regardless, excluding the additional uncertainty provided by fixed CS-US intervals does not meaningfully change calculations of temporal information in the suboptimal choice procedure and our subsequent reanalysis based on these calculations.

information theory to the temporal parameters of a procedure is an analytic practice that is guided only by the temporal structure of the procedure in order to quantify how much information signals embedded within the procedure convey. Time spent in the S- might therefore indirectly contribute to suboptimal choice through the effect it has on the relative temporal informativeness of TL stimuli for the suboptimal and optimal alternatives (i.e., by contributing to C). However, this does not mean that the S- *per se* influences suboptimal choice. Indeed, the temporal information-theoretic approach to conditioned reinforcement explicitly rejects the notion that stimuli that do not signal food directly impact responding (Shahan & Cunningham, 2015). Rather, time spent in the presence of the S- (but not the S- stimulus) might indirectly influence relative temporal informativeness based on its contribution to C.

Finally, note that varying signal conditions (i.e., whether or not TL stimuli differentially signal choice outcomes) will not influence C because the relation between TL stimuli and food delivery does not change any of the variables that determine C (see Equation 6). Thus, C remains constant throughout each of the signal conditions described below. Appendix A describes a slightly different method for calculating C when the suboptimal and optimal alternatives operate concurrently, as in a concurrent-chains suboptimal choice procedure.

Trial time. Whether or not the suboptimal or optimal TL stimulus conveys more temporal information depends entirely upon which TL stimulus is associated with a shorter delay to food (i.e., t). The average delay to food in the presence of a TL stimulus, t, is jointly determined by TL duration and the probability of food delivery following TL onset:

$$t = \frac{TL\ s}{pSr|TL} \quad (7),$$

where *p*Sr|TL is the probability of food delivery *following onset of the TL stimulus associated with food.* When probabilistic food for an alternative is signaled, *p*Sr|TL = 1 (by definition), and *t* for that TL stimulus is equal to TL duration. When probabilistic food for an alternative is unsignaled, *p*Sr|TL= *p*Sr and so *t* for that TL stimulus is longer than the TL duration by a factor of $1/pSr$. Because TL duration is the same for each alternative in suboptimal choice research, variations in *t* for suboptimal and optimal TL stimuli depend on variations in pSr|TL for that stimulus, which is precisely the variable manipulated across signal conditions. Thus, whether the suboptimal or optimal TL stimulus conveys more temporal information depends critically on signal conditions. It is important to note that the TL stimulus associated with the unsignaled alternative still conveys temporal information even though it is not perfectly predictive of each food delivery. Thus, just because a TL stimulus does not perfectly predict each food delivery for an alternative does not prevent it from conveying temporal information and therefore perhaps serving to some degree as a conditioned reinforcer.

Now that we have defined *C* and *t* in the suboptimal choice procedure, we can explore how relative temporal information conveyed by TL stimuli is affected by varying signal conditions (i.e., whether or not probabilistic food for a given alternative is signaled or unsignaled). Consider the case in which food is differentially signaled only for the suboptimal alternative. For the suboptimal alternative, *t* is 10 s / 1.0 = 10 s, whereas for the optimal alternative *t* is 10 s / 0.5 = 20 s. Thus, *C/t* for the suboptimal TL stimulus is 60 s / 10 s = 6 whereas *C/t* for the optimal TL stimulus is 60 s / 20 s = 3. Converting these *C/t* ratios into bits of temporal information using Equation 5, the TL stimulus for the suboptimal alternative conveys 2.6 bits of temporal information whereas the TL stimulus for the optimal alternative conveys 1.6 bits. Thus, when food is differentially signaled only for the suboptimal alternative, the food-predictive TL stimulus for that alternative is more temporally informative than the non-predictive TL stimulus for the optimal alternative.

When probabilistic food is differentially signaled only for the optimal alternative, *t* for the optimal alternative *t* is 10 s / 1.0 = 10 s, whereas *t* the suboptimal alternative is 10 s / 0.2 = 50 s. In this case, *C*/*t* for the optimal TL stimulus is 60 s / 10 s = 6, whereas *C*/*t* for the suboptimal TL stimulus is 60 s / 50 s = 1.2. Thus, when only the optimal alternative is signaled, the TL stimulus for the optimal alternative conveys more temporal information (2.6 bits) than the TL stimulus for the suboptimal alternative (0.26 bits).

When both alternatives are unsignaled, *t* for the suboptimal alternative is 10 s / 0.2 = 50 s, but for the optimal alternative *t* is 10 s / 0.5 = 20 s. Thus, *C/t* for the suboptimal TL stimulus is 60 s / 50 s = 1.2, whereas *C*/*t* for the optimal TL stimulus is 60 s / 20 s = 3. Under these signal conditions, the optimal TL stimulus conveys more temporal information (1.6 bits) than the suboptimal TL stimulus (0.26 bits).

Finally, under conditions in which both alternatives are signaled, *t* for suboptimal and optimal TL stimuli is 10 s / 1.0 = 10 s. Thus, *C/t* for both suboptimal and optimal TL stimuli are 60 s / 10 s = 6, and therefore TL stimuli for both alternatives convey the same amount of temporal information (2.6 bits).

To summarize, whether the TL stimulus for the suboptimal or optimal alternative provides more temporal information depends on the signal conditions (i.e., whether or not TL stimuli differentially signal choice outcomes for an alternative). TL stimuli that

Table 1. Comparison of Temporal Information for Each Signal Condition

	Suboptimal Signaled	Suboptimal Unsignaled
Optimal Signaled	$H_{sub} = H_{opt}$	$H_{sub} < \mathbf{H_{opt}}$
Optimal Unsignaled	$\mathbf{H_{sub}} > H_{opt}$	$H_{sub} < \mathbf{H_{opt}}$

differentially signal food have shorter values of t than TL stimuli that do not differentially signal food. Thus, TL stimuli for a signaled alternative provide more temporal information than TL stimuli for an unsignaled alternative. Interestingly, the critical role that $pSr|TL$ plays in relative temporal informativeness suggests a principled reason for why the predictive value hypothesis proposed by Zentall and colleagues has provided a useful heuristic to describe preference between TL stimuli in the suboptimal choice procedure. Specifically, the probability of food delivery given TL stimulus presentation (i.e., pSr|TL), which the predictive value hypothesis proposed is a critical variable determining conditioned-reinforcer value, has a major impact on the temporal variable (i.e., t) that determines whether the suboptimal or optimal TL stimulus conveys more temporal information.

Table 1 shows a nominal comparison of which alternative offers a more temporally informative TL stimulus in each of the four signal conditions described above. This table summarizes the preceding analysis of relative temporal information across signal conditions and serves as a rule-of-thumb for identifying which alternative provides a more temporally informative TL stimulus based on signal conditions. However, this nominal comparison does not specify the *degree* to which the TL stimulus for one alternative is more temporally informative than the other. The degree to which one TL stimulus conveys more temporal information than the other depends on the value of procedural variables that determine C *and* t (e.g., ITI duration, IL duration, TL duration, probability of food delivery, etc.). Varying these parameters within a signal condition will change the degree to which a TL stimulus for one alternative is more informative than the other, but will not affect the nominal difference presented in Table 1. For example, the TL stimulus for the suboptimal alternative will always be more temporally informative when only the suboptimal alternative is signaled, but the *degree* to which it is more informative depends on the values assumed by each of the temporal variables of the procedure that contribute to C and t.

However, it is important to note that varying the temporal parameters of the suboptimal choice procedure will not influence relative temporal informativeness when both alternatives are signaled. Changing variables like ITI duration, IL duration, TL duration, or probability of food delivery when both alternatives are signaled changes the *absolute* temporal information conveyed a TL stimulus, but leaves unaffected *relative* temporal information conveyed by TL stimuli between alternatives (which will always be $H_{sub}/H_{opt} = 1$ when TL stimuli for each alternative convey the same amount of temporal information, as in the both signaled condition).

Reanalysis: Gipson et al. (2009) to Present Day.

Using the method just described for calculating temporal information in the suboptimal choice procedure, we can now assess the degree to which suboptimal choice depends on the relative temporal information conveyed by TL stimuli for the suboptimal and optimal alternatives. However, we must first consider one additional factor that might contribute to the value of a TL stimulus as a conditioned reinforcer that is not currently captured by a temporal information approach to conditioning; namely, the amount of food signaled by a temporally informative stimulus.

Consider the procedure used by Zentall and Stagner (2011a) designed to mimic the kinds of choices humans make in gambling situations. Pigeons were presented with a choice between an alternative offering 10 food pellets 20% of the time with differential stimuli signaling choice outcomes (the suboptimal alternative), and an alternative offering 3 food pellets 100% of the time (the optimal alternative). Under these conditions, TL stimuli for the suboptimal and optimal alternatives convey the same amount of temporal information because each TL stimulus signals a 100% chance of food, resulting in equivalent values of t for both TL stimuli. Thus, pigeons should be indifferent between these alternatives if only temporal information is considered. However, Zentall and Stagner found a strong preference for the suboptimal alternative in this procedure (see also Hinnenkamp, Shahan, & Madden, 2017; Laude, Stagner, & Zentall, 2014; Laude, Beckmann, Daniels, & Zentall, 2014). Thus, preference for the suboptimal alternative in this gambling analog cannot be accounted for by temporal information alone. The simplest way to account for suboptimal preference in the gambling analog is to incorporate a role for the amount of food signaled by a stimulus as an additional factor that determines the overall value of that stimulus (as Zentall, 2016 suggest in the predictive value hypothesis). For example, 1 bit of temporal information about 10 food pellets might reasonably be more valuable than 1 bit of temporal information about 3 food pellets. Nevertheless, the temporal-informational theoretic approach to conditioning has previously not considered the role of reinforcement magnitude in the effects a food-predictive stimulus on behavior. As a first attempt to do so, we note that Killeen (1985) suggested that the function relating amount of food to value is nonlinear, such that $V = 1-e^{-\lambda A}$, where A is the amount of food and λ is a free parameter that determines the steepness of the value function. In order to incorporate a role for food amount into the value of TL stimuli, which we will term here "signal value" (i.e., V), we borrow the model proposed by Killeen (1985),

$$V = H\left(1 - e^{-\lambda A}\right) \qquad (8).$$

Equation 8 defines the value of a TL stimulus as a joint function of the temporal information it conveys and the amount of food it signals. Specifically, Equation 8 assumes that the asymptotic value of a TL stimulus is defined by the temporal information it conveys (i.e., *H*), and that larger food amounts generate values closer to this asymptote in a manner dependent upon λ. Note that when the amount of food signaled by TL stimuli for suboptimal and optimal alternatives is the same (as it is in the majority of experiments on suboptimal choice), *relative* signal value is equivalent to relative temporal information (i.e., *H*) because the parenthetical portion of Equation 8 is the same for both options and is therefore irrelevant.

In order to assess the ability of the temporal information-theoretic approach to characterize the role of TL stimuli in suboptimal choice, we reanalyzed suboptimal choice data using pigeons and starlings collected from Gipson et al., (2009) to present day[4] (earlier research on suboptimal choice will be considered in the next section). The

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[4] The synchronous condition from Vasconcelos et al., (2015) was excluded from this reanalysis because there was a delay between choice responses and presentation of the food-predictive signal. Although delays between choice responses and food-predictive signals is an important variable that influences suboptimal choice (see also McDevitt et al., 1997), this reanalysis is intended only to characterize the means by which food-predictive signals that follow choice responses influence suboptimal choice. Inserting a delay between choice responses and food-predictive signals introduces processes related to learning about instrumental contingencies that, while important, are beyond the scope of this paper (but see Gallistel, Craig, & Shahan, 2014 for an information-theory based approach to such problems).

top panel of Figure 3 shows obtained proportions of suboptimal choice in the experiments reanalyzed as a function of proportional signal value,

$$pSub = \frac{V_{sub}}{V_{sub} + V_{opt}} \qquad (9),$$

with λ=0.3 for studies employing differential food magnitudes. Overall, relative signal value provides a reasonable account of suboptimal choice in the experiments reanalyzed. Generally speaking, choice appears to track relative signal value. The range of values obtained for relative signal value resulted primarily from variations in procedural variables that influence relative temporal informativeness both within and between experiments, such as the probability and duration of the S- for the suboptimal alternative (e.g., Fortes et al., 2016; Vasconcelos et al., 2015), TL duration for the optimal alternative (e.g., Zentall & Stagner, 2011b), and the overall probability of food delivery for either alternative (e.g., Gipson et al., 2009; Stagner & Zentall, 2010; Zentall et al., 2015). The orderly relation between suboptimal choice and relative signal value presented in the top panel of Figure 3 suggests that the effect these variables have on suboptimal choice might be realized through their effect on temporal information. Further, when TL stimuli for suboptimal and optimal alternatives provide the same amount of temporal information, as in the gambling-analog experiments (Hinnenkamp, Shahan, & Madden, 2017; Laude, Stagner, & Zentall, 2014; Laude, Beckmann, Daniels, & Zentall, 2014; Zentall & Stagner, 2011a), preference develops for the TL stimulus that signals the greater amount of food.

As indicated by the steep rise in preference for the suboptimal alternative depicted in the top panel of Figure 3, even a slightly more valuable signal (i.e., TL stimulus) for the suboptimal alternative can result in a drastic increase in preference for that alternative. This steep rise in suboptimal preference might result from the discrete-trial choice procedure used to study suboptimal choice in the experiments reanalyzed. Indeed,

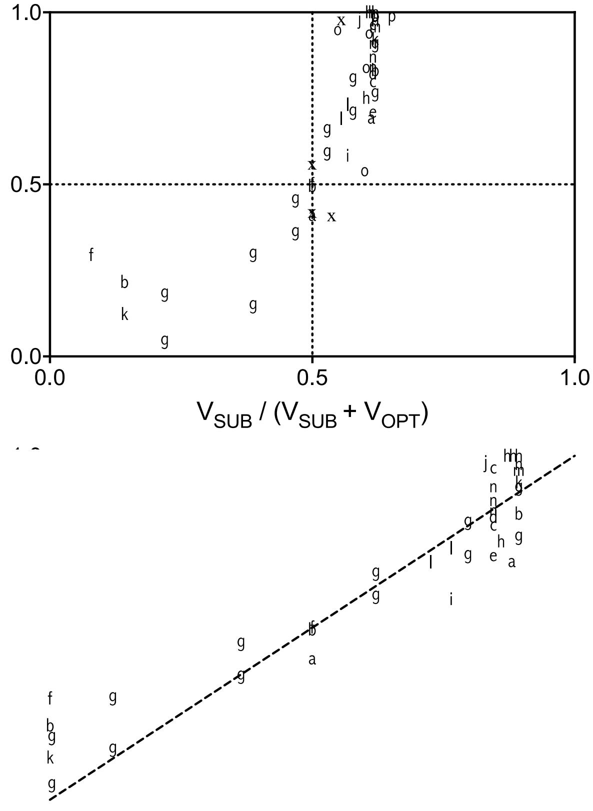

Figure 3. Top Panel: Proportion suboptimal choice as a function of relative signal value (i.e., Equation 9). Bottom Panel: Proportion suboptimal choice as a function of relative signal value with a sensitivity parameter (i.e., Equation 10). Legend: a = Gipson et al., 2009; b = Stagner et al., 2012; c = Laude, Stagner, & Zentall, 2014; d = Zentall & Stagner, 2011a; e = Laude, Beckmann, Daniels, & Zentall, 2014; f = Smith & Zentall, 2015; g = Zentall & Stagner, 2011b; h = Vasconcelos et al., 2015; i = Laude et al., 2012; j = Pattinson et al., 2013; k = Stagner & Zentall, 2010; l = Zentall et al., 2015; m = Stagner et al., 2011; n = Hinnenkamp et al., 2017; o = Fortes et al., 2016; p = Fortes et al., 2017; z = Zentall et al., 2017.

Mazur (2010) found that discrete-trial choice procedures tend to generate strong preference for the more valuable alternative regardless of the degree to which it is more valuable, which is a choice strategy in stark contrast to matching choice allocation to the relative value of each alternative (see also, Killeen, 2015). Further, some research indicates that preference for a more favorable reinforcement schedule over a less favorable schedule is stronger when those schedules are trained independently and tested in probe-choice trials (e.g., Crowley & Donahoe, 2004; see also, Gallistel & Gibbon, 2000). The suboptimal choice procedure bears similarity to this kind of choice structure in that a majority of trials are forced-exposure trials (i.e., independent training for each alternative) and choice is only occasionally probed in free-choice trials. Thus, hypersensitivity of suboptimal choice to relative signal value might result from (1) the use of a discrete-trial choice procedure, and (2) independent exposure to suboptimal and optimal alternatives during forced-exposure trials, each of which have been shown to encourage near-exclusive preference for the more valuable alternative (i.e., opting), rather than matching (i.e., allocating). Regardless of the source of hypersensitivity to relative signal value, it appears necessary to include a sensitivity parameter for signal value in order to better characterize how relative signal value influences suboptimal choice,

$$pSub = \frac{V_{sub}^{a}}{V_{sub}^{a} + V_{opt}^{a}} \qquad (10),$$

where all terms are as in Equation 9 and a is a parameter corresponding to sensitivity of suboptimal choice to relative signal value. Equation 10 was fit to all post-Gipson et al., (2009) suboptimal choice data (i.e., the same data in the top panel of Figure 3) using least-squares regression. The bottom panel of Figure 3 depicts the results of this fit with obtained parameter values a = 4.3 and λ = .36 (for studies with differential reinforcement magnitudes) and $R^2 = .79$. Overall, Equation 10 provides a reasonable account of the data and might therefore provide a means to understand how TL stimuli influence suboptimal choice from a temporal information-theoretic perspective[5].

Pre-Gipson et al., (2009): IL and TL Effects on Suboptimal Choice

In this section we examine the ability of Equation 10 to account for research on suboptimal choice conducted prior to the Gipson et al., (2009) study. There are a couple of important procedural differences between earlier and more recent suboptimal choice studies that reveal variables that appear to influence suboptimal choice and are not captured by Equation 10. The resulting failure of Equation 10 to accurately account for some of this earlier research on suboptimal choice (described below) suggests that relative signal value is not the sole determinant of choice, as Equation 10 assumes.

While more recent research on suboptimal choice (i.e., post-Gipson et al., 2009) used a discrete-trial choice procedure, earlier research used a more traditional concurrent-chains procedure in which the suboptimal and optimal alternatives operated concurrently. The optimal alternative provided food 100% of the time whereas the suboptimal alternative provided a lower chance of food (usually 50%) with TL stimuli that differentially signaled whether or not food would be delivered. Under these conditions, $p\text{Sr}|\text{TL} = 1$ for both suboptimal and optimal TL stimuli, and for this reason each TL stimulus has the same value of t. Thus, suboptimal and optimal TL stimuli convey the

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[5] Note that a softmax (i.e., logistic) decision rule can also be successfully used to generate choice proportions from suboptimal choice procedures using relative signal value as described above. However, we have chosen a matching-law decision rule because its makes better contact with the widespread use of such a decision rule in the concurrent chains literature. There is also some empirical evidence that the matching rule might better describe human decision making than the softmax rule (Worthy, Maddox, & Markman, 2008).

same amount of temporal information and Equation 10 therefore predicts indifference between suboptimal and optimal alternatives in numerous experiments conducted prior to Gipson et al., (e.g., Dunn & Spetch, 1990; Fantino et al., 1979; Spetch et al., 1990; Spetch et al., 1994). The problem is that pigeons often preferred the *optimal* alternative in these experiments (e.g., Dunn & Spetch, 1990; Spetch et al., 1990; Fantino et al., 1979; McDevitt et al., 1997; Spetch et al., 1994). Thus, Equation 10 often over-predicts preference for the suboptimal alterative when applied to earlier research on suboptimal choice. The question is: what was different between earlier and more recent suboptimal choice research that might explain why Equation 10 adequately accounts for more recent research but often does not account for earlier research?

The most noteworthy procedural differences between earlier and recent research on suboptimal choice are (1) relatively long VI IL schedules often used in earlier research, compared to the standard FR 1 IL schedule used in more recent research (i.e., post-Gipson et al., 2009), and (2) the wide array of TL durations used in earlier research compared to the somewhat standard 10 s TL duration used in more recent research. Perhaps the reason pigeons often preferred the optimal alternative, rather than choosing equally between alternatives as Equation 10 predicts, is that IL and TL durations influence suboptimal choice. Indeed, a variety of earlier studies on suboptimal choice directly explored the role of IL and TL duration on suboptimal choice (e.g., Dunn & Spetch, 1990; Kendall, 1985; Spetch et al., 1990; Spetch et al., 1994). The conclusion often drawn from these studies is that suboptimal choice is positively related to TL duration and negatively related to IL duration (see McDevitt et al., 2016).

Next, we will take a closer look at studies directly exploring the effect of IL and TL duration on suboptimal choice. The possible effects of IL and TL duration on suboptimal choice are of special importance for two reasons. First, some have questioned the validity of these effects because (1) key biases arising from suboptimal and optimal alternatives being defined by key location might have distorted measures of suboptimal choice (Smith & Zentall, 2016), and (2) the effects of IL and TL duration on suboptimal choice were often inconsistent between experiments (Stagner et al., 2012; Zentall, 2016). Thus, a reanalysis of all studies exploring the role of IL and TL duration on suboptimal choice might clarify whether there is sufficient evidence for their effects on suboptimal choice.

Second, and most important for present purposes, studies that varied IL and TL durations in the suboptimal choice procedure did so under conditions in which TL stimuli for both the suboptimal and optimal alternatives conveyed the same amount of temporal information (i.e., t was the same for TL stimuli for each alternative). Recall from the previous section that when t is identical between suboptimal and optimal alternatives, and therefore each TL stimulus conveys the same amount of temporal information, variations in IL and TL duration do not influence *relative* signal value (i.e., Equation 10). Thus, the possible effects of IL and TL duration on suboptimal choice pose a challenge to the temporal information-theoretic approach described above. Further, the possible effects of IL and TL duration on suboptimal choice are fundamentally different from the effects these variables have on choice in standard concurrent-chains research (i.e., IL and TL effects), which Shahan & Cunningham (2015) showed can indeed be captured by variations in relative signal value. Appendix B provides a detailed description of why IL and TL durations change relative signal value in standard concurrent-chains procedures but not in the concurrent-chains procedure employed in earlier research on suboptimal choice (discussed in detail below).

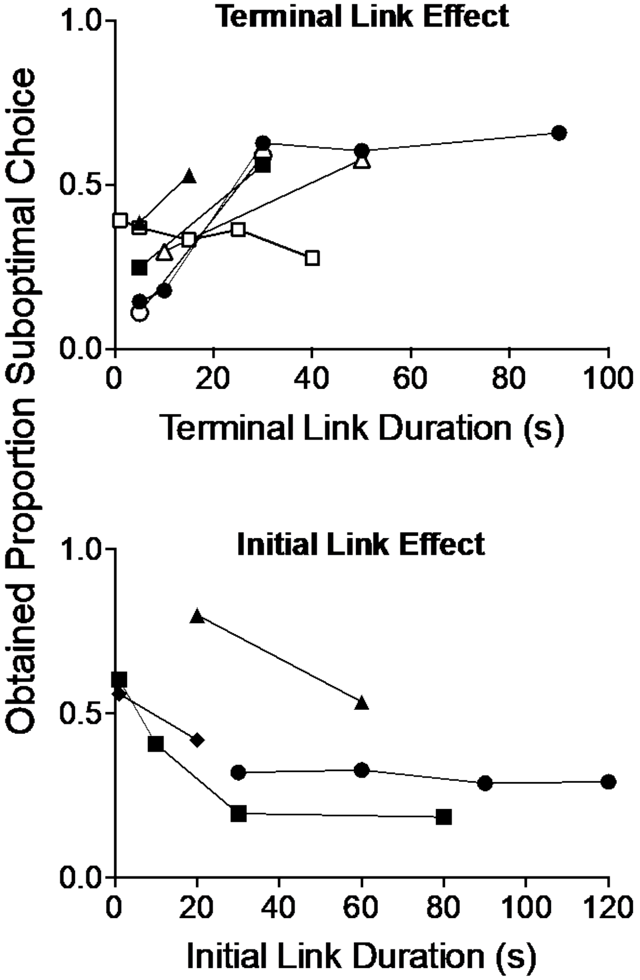

Figure 4. The top panel depicts a reanalysis of all suboptimal choice experiments that have manipulated terminal-link duration. Closed circles, squares, and triangles represent Spetch et al., (1990; Experiment 1), Spetch et al., (1990; Experiment 2), and Kendall (1985; Experiment 2), respectively. Open circles, squares and, triangles represent Spetch et al., (1994; Experiment 3), Dunn & Spetch (1990; Experiment 1), and Spetch et al., (1990; Experiment 3), respectively. The bottom panel depicts a similar reanalysis but for studies that have manipulated initial-link duration. Closed circles, squares, triangles, and diamonds represent Dunn & Spetch (1990; Experiment 1), Dunn & Spetch (1990; Experiment 3), Kendall (1985; Experiment 2), and Zentall et al., (2017; Experiment 1), respectively.

Terminal-Link Effect. Spetch et al., (1990) assessed suboptimal choice across a variety of TL durations ranging from 5 s to 90 s, importantly with a FR 1 IL schedule. Spetch et al. found that pigeons preferred the optimal alternative at short TL durations (i.e., 5 to 10 s) and were approximately indifferent between suboptimal and optimal alternatives at longer TL durations (i.e., 30 s or greater). This positive relation between allocation to the suboptimal alternative and TL duration with a FR 1 IL schedule has been found in numerous other studies (e.g., Kendall, 1985; Spetch et al., 1994). However, Dunn and Spetch (1990) did not find an effect of TL duration on suboptimal choice across a relatively wide range of TL durations (1 s to 40 s) using a variable-interval (VI) 60 s IL schedule. Thus, the positive relation between TL duration and suboptimal choice appears to depend on IL duration (though the role of IL duration in the sensitivity of suboptimal choice to TL duration has never been addressed directly and certainly warrants future research).

In the top panel of Figure 4 we present a reanalysis of all experiments that have directly assessed the effect of TL duration on suboptimal choice in which both suboptimal and optimal alternatives provide TL stimuli that differentially signal food. As shown in the top panel of Figure 4, there is fairly robust evidence that increasing TL duration increases preference for the suboptimal alternative (at least when FR 1 IL schedules are used). Thus, TL duration appears to influence suboptimal choice even when relative signal value is constant.

Initial-Link Effect. In the first experiment to directly assess the effect of IL duration on suboptimal choice, Kendall (1985) found that VI 20 s IL schedules supported more suboptimal choice than did VI 60 s IL schedules. However, results from this experiment were not particularly convincing because only 2 pigeons were used. Dunn and Spetch (1990) subsequently investigated the effect of IL duration on suboptimal choice across a wide range of IL values. In Experiment 1, Dunn and Spetch found that suboptimal choice was unaffected by variations in IL duration ranging from VI 30 s to a VI 120 s. However, in Experiment 3, Dunn and Spetch found that suboptimal choice increased at extremely short IL durations. Specifically, pigeons were approximately indifferent between suboptimal and optimal alternatives with FR 1 and VI 5 s IL schedules, but preferred the optimal alternative at longer IL durations (i.e., VI 20 s or longer). This result suggests that very short IL durations support suboptimal choice, and that even modest increases in IL duration drastically decrease suboptimal choice.

In the bottom panel of Figure 4, we present a reanalysis of all experiments that have directly assessed the impact of IL duration on suboptimal choice. Although the data are limited, this reanalysis suggests that increasing IL duration tends to decrease suboptimal choice. Further, the possible effect that IL duration has on the sensitivity of suboptimal choice to TL duration (Dunn & Spetch, 1990) suggests that IL duration might also indirectly influence suboptimal choice. However, the suboptimal choice literature would certainty benefit from future research carefully exploring both the direct and indirect effects of IL duration on suboptimal choice (see Zentall et al., 2017 for a recent attempt to clarify the direct effects of IL duration on suboptimal choice).

Summary. Our reanalysis suggests that there is currently reasonable evidence for a positive relation between suboptimal choice and TL duration and a negative relation between suboptimal choice and IL duration[6]. As others have noted (Spetch et al., 1994; McDevitt et al., 2016), these findings suggest that suboptimal choice is supported by short IL durations in conjunction with relatively long TL durations. However, because Equation 10 is unaffected by IL and TL durations when TL s for each alternative are the same duration (as in the experiments reanalyzed in Figure 4), relative temporal information alone cannot explain the fact that short IL durations and long TL durations support suboptimal choice, nor can it capture changes in suboptimal choice as a function of IL and TL durations as depicted in Figure 4. Thus, in the next section we consider one approach to formalize the role of IL and TL duration in suboptimal choice within the information-theoretic framework defined by Equation 10.

Temporal Information, Primary Reinforcement Rate, and their Competition

Thus far, our approach has assumed, like others (e.g., Zentall, Laude, Stagner, & Smith, 2015), that suboptimal choice depends only on the value of TL stimuli that follow choice responses. However, the fact that IL and TL durations affect suboptimal choice without affecting relative signal value (i.e., Equation 10) challenges the notion that relative signal value is the sole determinant of suboptimal choice. Given the ubiquitous role that relative primary reinforcement rate has on choice (see Davison & McCarthy,

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[6] Note that the IL and TL effects depicted in Figure 4 are opposite to those found in more typical concurrent-chains research. In the suboptimal choice literature, choice approaches indifference as IL duration *decreases* whereas in the concurrent-chains literature choice approaches indifference as IL duration *increases*. Further, in the suboptimal choice literature preference for the more favorable alternative becomes stronger as TL duration *decreases*, whereas in the concurrent-chains literature preference for the more favorable alternative becomes stronger as TL duration *increases*. Thus, the effects of IL and TL duration on suboptimal choice indeed appear to be fundamentally different from those in concurrent-chains research. This discrepancy further warrants our suggestion below that a separate mechanism (i.e., other that relative signal value) is required to account for IL and TL effects in suboptimal choice procedures.

1988), it seems plausible to assume that relative primary reinforcement rate also contributes to suboptimal choice independent of relative signal value, and therefore these two sources of control might compete to determine choice. Perhaps IL and TL durations influence suboptimal choice by influencing competition between relative primary reinforcement rate and relative signal value.

Based on the wide variety of research showing that choice between two schedules of primary reinforcement matches the relative rates of reinforcement for those alternatives (see Baum, 1974), we express the impact of relative primary reinforcement rate on suboptimal choice as

$$pSub = \frac{R_{sub}^{b}}{R_{sub}^{b} + R_{opt}^{b}} \qquad (11),$$

where R is the rate of primary reinforcement for each alternative (identified by the subscript) and b is a free parameter that determines the sensitivity of choice to relative primary reinforcement rate. Equation 11 is simply a version of the generalized matching law but without a term for bias (McDowell, 2005). In order to formalize competition between relative signal value and relative primary reinforcement rate, we can simply include a weighting parameter, w, that is applied to relative signal value (i.e., Equation 10) and its complement, 1-w, that is applied to relative primary reinforcement rate (i.e., Equation 11),

$$pSub = w\frac{V_{sub}^{a}}{V_{sub}^{a} + V_{opt}^{a}} + (1 - w)\frac{R_{sub}^{b}}{R_{sub}^{b} + R_{opt}^{b}} \qquad (12).$$

When $w = 1$, choice is governed solely by relative signal value. When $w = 0$, choice is governed solely by relative primary reinforcement rate. Thus, Equation 12 describes one way to incorporate a role for primary reinforcement rate within the temporal information-theoretic approach to suboptimal choice. Within the framework defined by Equation 12, the effect of IL and TL duration on suboptimal choice might be realized through *w*. The question now becomes: how can IL and TL durations influence competition between relative signal value and relative primary reinforcement rate in a conceptually plausible way?

Our inclusion of *w* in Equation 12 was inspired by Dayan, Niv, Seymour, and Daw (2006). Dayan et al. designed a reinforcement-learning model to describe competition between Pavlovian and instrumental behaviors in order to account for maladaptive outcomes that might result from such competition (e.g., negative automaintenance and the classic examples of "misbehavior" reported by Breland and Breland, 1961). Indeed, the critical role of Pavlovian, food-predictive signals (i.e., TL stimuli) in suboptimal choice suggests that it too might be considered a form of misbehavior resulting from an animal's pre-occupation with food-predictive signals (i.e., a CS) that interferes with more adaptive, instrumental behaviors that are necessary to obtain the US it predicts. These maladaptive patterns of behavior are made possible when Pavlovian-related behaviors are put in direct competition with instrumental behaviors that are required to obtain food. For example, in negative automaintenance in pigeons, the Pavlovian behavior of pecking a signal for food is put in direct competition with the instrumental behavior of not pecking that signal to obtain food. In suboptimal choice, the behavior of obtaining/approaching more temporally informative signals (i.e., choice for the suboptimal alternative) is put in direct competition with the obtaining/approaching richer sources of primary reinforcement (i.e., choice for the optimal alternative). Only when food-predictive signals hold more weight as a determinant of behavior than food itself can maladaptive patterns of behavior emerge.

According to the reinforcement-learning model proposed by Dayan et al., the strength of the Pavlovian behavior (e.g., pecking an illuminated key that predicts food) is determined by the value of the Pavlovian CS while the strength of the instrumental behavior (e.g., not pecking a key in order to receive food) is determined by the value of the reward it produces. Most important for present purposes, the value of the Pavlovian CS is given a weight, *w*, while value of the instrumental reward (i.e., the instrumental advantage) is given its complement, 1-*w*. This weighting mechanism determines the degree to which animals are biased to engage in Pavlovian behaviors at the expense of more adaptive, instrumental behaviors. Thus, higher values of *w* result in Pavlovian behavior that is more likely to outcompete instrumental behavior.

To illustrate how Pavlovian-instrumental competition works with this model, and importantly how it might be used to understand competition between signal value and primary reinforcement rate as a determinant of suboptimal choice, consider an example in which an animal is placed in a maze and a CS is turned on in one location and a US is placed in another location (see Figure 2 from Dayan et al., 2006). The question is: what is the likelihood that the animal approaches the CS instead of the US? As Dayan et al. pointed out, the answer to this question depends critically on where in the maze the animal is located when the choice is made. It is more likely that the animal approaches the CS instead of the US when it is closer to the CS relative to the US. Alternatively, the likelihood of approaching the CS instead of the US declines when the animal is closer to the US relative to the CS. The weighting parameter, *w,* influences the degree to which approach to the CS is more likely than approach to the US at any given location in the maze. With higher values of *w*, the CS has much greater influence throughout the maze, resulting in a greater likelihood of approaching the CS instead of the US even when the animal is relatively far away from that CS. With lower values of *w*, the CS has influence only in its immediate vicinity, and so approach to that CS is likely only when the animal is especially close to it relative to the US. Thus, the Dayan et al. model suggests that competition between approaching the CS or the US depends on (1) the Pavlovian bias as indexed by *w*, and (2) the relative spatial proximity of the CS and US at the choice point. From this perspective, maladaptive outcomes that result from approach and attraction to a CS result largely from the strong gravitation pull of the CS when in close proximity to it relative to the US, and the degree to which relative proximity influences the decision to approach the CS or US depends on *w*.

In order to apply this notion to suboptimal choice, we suggest that IL and TL durations influence suboptimal choice by changing the relative temporal (rather than spatial) proximity of the temporally informative signals and food at the choice point. We define "choice point" in the suboptimal choice procedure as the moment IL stimuli are illuminated and the choice phase begins (i.e., when we ask the animal to choose between suboptimal and optimal alternatives). According to this perspective, animals are biased to use signal value rather than primary reinforcement rate to make decisions between suboptimal and optimal alternatives when the temporally informative signals are much closer in time than food itself at the choice point. Thus, the weighting parameter, *w,* in Equation 12 might be considered a variable that is governed by the ratio of the delay to food relative to the delay to the temporally informative signals,

$$w = \frac{1}{1 + e^{-\beta\left(\frac{D_f}{D_s} - m\right)}} \quad (13),$$

where D_s is the average delay to a temporal informative signal (i.e., TL stimulus) at the choice point, D_f is the average delay to food at the choice point, β is a free parameter that determines the sensitivity of w to the delay ratio, and m is a free parameter that determines the delay ratio at which $w = .5$. Values of m might be interpreted as a bias for using primary reinforcement rate rather than signal value to make choices between suboptimal and optimal alternatives (i.e., higher values of m indicate that the temporally informative signals have to be much closer in time relative to food before signal value contributes as much to choice as primary reinforcement rate). Generally speaking, when a temporally informative signal is substantially closer in time relative to food itself at the choice point (i.e., when D_f/D_s is relatively large), w is close to 1 and choice is governed primarily by relative signal value. Alternatively, when the temporally informative signals and food are equidistant at the choice point (i.e., when D_f/D_s close to 1), w is close to 0 and choice is governed primarily by relative primary reinforcement rate.

Inserting Equation 13 into Equation 12 provides a means to capture the IL and TL effects on suboptimal choice discussed earlier. Consider first the effect of increasing TL duration with a short IL duration (e.g., an FR 1 IL schedule). As TL duration increases, the delay to food at the choice point increases whereas the delay to the temporally informative signals remains constant (because IL duration does not change). Thus, at very short TL durations, D_f/D_s is close to 1 and w is therefore close to 0. Under these conditions choice should depend largely on relative primary reinforcement rate and preference for the optimal alternative is predicted. At longer TL durations, the signals are situated much closer in time than food at the choice point. Thus, D_f/D_s increases and w

subsequently approaches 1. Under these conditions, relative signal value should become the stronger determinant of choice. However, when IL duration is relatively long, as in the VI 60 s schedules used in Dunn and Spetch (1990), increasing TL duration (e.g., from 1 s to 40 s) should not have a strong influence on w because D_f/D_s never grows much larger than 1. In order for D_f/D_s to increase meaningfully above 1 with long IL durations (and thus for w to approach 1), TL duration would have to be exceptionally long to compensate for the relatively long IL duration. Thus, Equation 13 can capture the finding that suboptimal choice is sensitive to TL duration only with relatively short IL durations.

Equation 13 can also capture the finding that longer IL durations increase preference for the optimal alternative. With short IL durations and long TL durations (as in Dunn & Spetch, 1990; Experiment 3), the temporally informative signals are much closer in time at the choice point than food itself. In this case, D_f/D_s is much greater than 1 and so choice should be governed primarily by relative signal value because w is close to 1. As IL duration increases and TL duration is held constant, D_f/D_s approaches 1 and preference for the optimal alternative should increase because relative primary reinforcement rate becomes the stronger determinant of choice (because w approaches 0 as D_f/D_s approaches 1). Thus, the weighting mechanism defined by Equation 13 describes IL and TL effects on suboptimal choice based on how they influence the competition between relative signal value and relative primary reinforcement rate as a determinant of choice. According to Equation 13, suboptimal choice emerges when we (as experimenters) ask the animal to choose at a point in time when they are strongly attracted to Pavlovian signals even if it means, as a result, they will miss out on food that might have been available later (much like an animal in the maze example from Dayan et al., 2006 would approach the CS instead of the US if it was placed in the maze much closer to the CS than the US).

Equation 12 with *w* calculated according to Equation 13 was fit to all data on suboptimal choice using pigeons and starlings in order to assess its viability as a general account of suboptimal choice (i.e., we used all data presented in Figure 3 and included data collected prior to the Gipson et al., 2009 study[7]). Obtained parameter values from the model fit were: a=4.4, b=1.4, $\beta = 1.4$, $m = 1.8$, and $\lambda = .37$ (for studies employing differential reinforcement magnitudes[8]), with $R^2 = .85$. Data from Spetch et al., (1990) and Dunn & Spetch (1990, Experiment 3) were fit separately from the rest of the data because these studies required different parameter values for the weighting function in

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[7] Excluded Experiments: We did not include any conditions or experiments for which a group mean could not be obtained. This happened in experiments in which certain procedural details, such as IL and TL durations, were different for each subject (Experiment 1, Phase 2: Dunn & Spetch, 1990; Experiment 2, Phase 2: Spetch & Dunn, 1987; Experiment 1, Unsignaled condition: Spetch et al., 1990). Further, only the "No Delays" condition from McDevitt et al., 1997 was included because all other conditions included a delay between choice responses and food-predictive signals (see Footnote 2). Finally, we excluded any experiment or condition that generated a negative value for temporal information signaled by a TL stimulus (Experiment 2, Unsignaled condition: Spetch et al., 1990; Experiment 3, Unsignaled condition: Spetch et al., 1994; Kendall, 1974; Experiment 1, Unsignaled condition: Kendall, 1985). A negative value for temporal information presents a challenge to the way in which Shannon entropy is applied to the distribution of food in time in Pavlovian conditioning procedures (e.g., Gallistel & Balsam, 2009; Balsam et al., 2010), and in our extension of it to the suboptimal choice procedure because it is impossible for a signal to increase uncertainty beyond the basal uncertainty (by definition). We discuss this issue more in the Limitations section below.

[8] Lambda is only relevant for those studies that arranged different reinforcement magnitudes between suboptimal and optimal alternatives, as in the gambling analog experiment described above. These gambling-analog studies include: Hinnenkamp et al., 2017; Laude J. R., Beckmann, J. S., Daniels, C. W., & Zentall, T. R. (2014); Laude J. R., Beckmann, J. S., Daniels, C. W., & Zentall, T. R. (2014); Zentall & Stagner, 2011a. Thus, the lambda parameter was used for only these studies, which constitute 7 of the 110 data points reanalyzed.

order to more accurately describe the data. Obtained parameter values for this separate fit were: a=4, b=2.1, $\beta = .53$, $m = 13$, with $R^2 = .79$ (note that λ is omitted because reinforcement magnitude was the same for both alternatives in these studies). Thus, the most noteworthy difference in obtained parameter values for the fit to Spetch et al., (1990) and Dunn & Spetch (1990; Experiment 3) and the fit for the rest of the data was that m had to be considerably higher and β lower to adequately describe the Spetch et al., (1990) and Dunn & Spetch (1990) data. In terms of the model, these differences suggest that pigeons in these studies appeared to have a strong bias to use relative primary reinforcement rate to choose between alternatives even when the temporally informative signals were considerably closer in time than food (i.e., even when food-predictive signals were 13 times more immediate than food). Further, smaller values of β indicate that pigeons in these studies were relatively insensitive to the relative delay ratio (i.e., D_f/D_s). It is currently unclear why the weighting mechanism would differ for these two studies compared to all other suboptimal choice studies.

Figure 5 depicts the match between obtained proportion of suboptimal choice and predicted proportion of suboptimal choice based on the model fits just described. As shown in Figure 5, the model defined by Equations 12 and 13 provides a reasonable account of existing data on suboptimal choice in pigeons and starlings. Relative signal value alone can adequately characterize more recent data on suboptimal choice (as shown in Figure 3) while the inclusion of relative primary reinforcement rate and its competition with relative signal value based on D_f/D_s can accurately capture earlier research on suboptimal choice. Further, the expansion of the temporal-informational approach represented by Equations 12 and 13 does not negatively impact its ability to account for the basic findings from standard concurrent-chains schedules outside of the context of suboptimal choice (see *Appendix C* for discussion).

The model defined by Equations 12 and 13 was developed primarily to account for the effects of IL and TL duration on suboptimal choice. However, further evidence for the need to include a role for primary reinforcement rate and its competition with signal value might come from species differences in suboptimal choice between rats and pigeons (e.g., Trujano & Orduna, 2015). The fact that rats do not always show suboptimal choice under nearly identical conditions to those that generate suboptimal choice in pigeons suggests that choice in rats might be governed more by relative primary reinforcement rate than relative signal value. Interestingly, the model proposed here (i.e.,

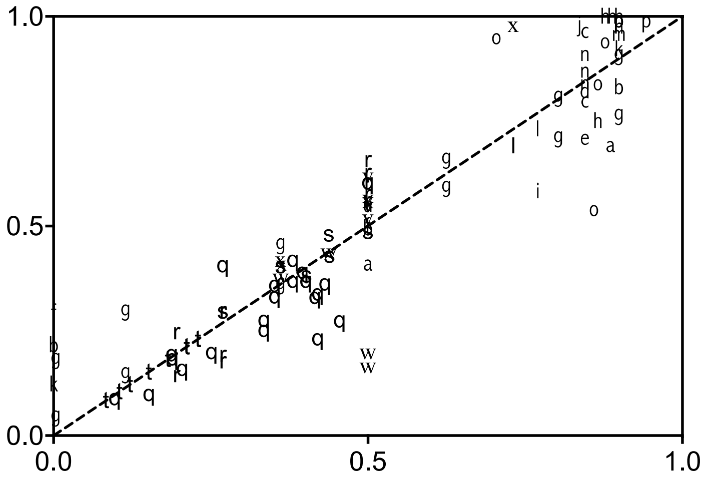

Figure 5. Predicted versus obtained proportion of suboptimal choice is plotted for all experiments reanalyzed. Each data point represents a group mean from an experiment or a condition within an experiment. Legend: symbols for the experiments depicted are the same as in Figure 3. Symbols for additional experiments are: q = Dunn & Spetch, 1990; r = Spetch et al., 1990; s = Fantino et al., 1979; t = Spetch & Dunn, 1987; u = McDevitt et al., 1997; v = Spetch et al., 1994; w = Kendall, 1985.

Equations 12 & 13) might provide a means to account for such species differences through *w*.

Perhaps the reason pigeons more readily engage in suboptimal choice than rats is because the stimulus-modality used to signal food is better suited to the pigeon's evolutionary history than to the rat's. Specifically, research on suboptimal choice in pigeons has exclusively used visual stimuli to signal food. Visual stimuli are highly salient to pigeons and, when localized, provide them with the opportunity to engage in species-specific behaviors that are directed towards the signal for food (i.e., sign-tracking). However, the use of visual and auditory stimuli with rats does not provide them with a similar opportunity to engage in its species-specific responses that are directed towards signals for food. Instead, manipulable objects that predict food, such as a lever that enters the chamber soon before food is delivered, tend to elicit species-specific, sign-tracking responses in rats much like visual stimuli for pigeons (Boakes, 1977; Robinson, Yager, Cogan, & Saunders, 2014). Interestingly, the only successful report of suboptimal choice in rats used lever presentations to signal food for choice responses (Chow et al., 2017). Thus, it is possible that providing animals with the opportunity to engage in these species-specific, sign-tracking responses plays a critical role in biasing them to respond for and pay more attention to food-predictive signals (Chow et al., 2017). In other words, variables related to the incentive salience of food-predictive signals (Robinson & Berridge, 1993), such as stimulus modality and its ability to support sign-tracking responses, might influence the degree to which temporally informative signals influence choice at the expense of primary reinforcement rate. Such an effect would be realized through *w* (see Beckman & Chow, 2015, and Lesiant et al., 2014, for discussions on the role of Pavlovian weighting, *w*, and its relation to sign-tracking and competition with instrumental, goal-directed behavior). Thus, the model described here might also provide a starting point to understand species differences in suboptimal choice, which at present is an issue that is not readily accounted for by other hypotheses of suboptimal choice (e.g., the evolutionary pressures that shape decision-making strategies resulting in suboptimal choice should reasonably be similar for both avians and rodents).

Limitations and Unanswered Questions

One limitation of the information-theoretic approach proposed here is that under certain conditions the temporal information conveyed by a TL stimulus can assume a negative value. In the suboptimal choice procedure, this problem arises for relatively long TL stimuli (i.e., long *t*) in conjunction with an especially short value of *C* (see Footnote 6 for a list of experiments that were excluded for this reason). A negative value generated by Equation 5 means that uncertainty about time to food in the presence of the TL stimulus is greater than the basal uncertainty. This is a problem because basal uncertainty, which can be conceptualized as the channel through which signals are conveyed, defines the maximum amount of uncertainty associated with a probability distribution (i.e., the channel). Any signal communicated within that channel cannot increase uncertainty above and beyond the uncertainty associated with that channel without any signal (i.e., the basal uncertainty), by definition. Thus, the way in which entropy is applied to the temporal distribution of reinforcement in a conditioning procedure, as described here and elsewhere (e.g., Balsam et al., 2010), needs adjustment in order to properly quantify temporal information in a way that does not yield negative values for stimuli that signal an increase in time to reinforcement above the overall average time to reinforcement. While it is currently unclear how this problem should be solved, we suspect that the problem is related to an improper quantification of basal uncertainty, which we and others (e.g., Balsam et al., 2010) take as the average inter-food interval (i.e., *C*) in the session. Specifically, the issue might be related to the fact that a simple average rate of all food deliveries in the session does not accurately describe the temporal regularity of food in the environment, and as a result basal uncertainty is not properly characterized and quantified. However, it is important to note that only five of 115 experimental conditions (i.e., conditions within an experiment or experiments within a publication) were excluded from our reanalysis because of negative-information values.

A second potential limitation is our assumption that while an S- does not contribute at all to choice, a stimulus associated with a very low probability of food does (e.g., a stimulus that is followed by food only 1% of the time). Described in terms of the present model, a stimulus that conveys even a marginal amount of temporal information (e.g., .01 bits) should have a measurable impact on choice whereas a stimulus that does not convey any temporal information should not. Whether or not animals treat such stimuli differently than a stimulus that provides no temporal information (e.g., an S-) remains unclear, but this is an interesting conceptual and empirical question. Further, it is important to note that this issue arises with every theory of conditioned reinforcement (e.g., within the delay reduction framework, should a stimulus that only marginally reduces the overall delay to food be considered any better than a stimulus that does not reduce the delay at all?).

A third potential limitation is our assumption that the weight given to relative signal value and relative primary reinforcement rate depends on the delay to food relative to the delay to temporally informative signals (D_f/D_s) only at the moment IL stimuli are illuminated (which we define as the "choice point"). While this assumption is reasonable when FR 1 IL schedules are used (as in the large majority of suboptimal choice research), it is less clear how to define the choice point when longer IL schedules are used. In the case of longer IL schedules, D_f/D_s might change dynamically as the IL progresses, and therefore w might change as the IL progresses. Specifically, D_f/D_s could increase as the IL progresses and the temporally informative TL stimuli grow closer on the temporal horizon. If true, this would suggest that choice during the IL should vary systematically as the IL progresses (specifically, that suboptimal choices should become more frequent as the IL progresses). Whether or not suboptimal choice varies systemically as the IL progresses is currently unclear because the few studies that used relatively long IL durations only report average suboptimal choice across the entire IL choice phase (i.e., they do not report the dynamics of choice across the IL). However, this is an interesting question that is directly related to (1) the conceptual question of how to define "choice point", and (2) whether or not a weighting mechanism like that defined in Equation 13 should be dynamic rather than static.

Finally, our method for calculating relative temporal informativeness considers only cases in which TL stimuli are perfectly correlated (i.e., signaled) or uncorrelated (i.e., unsignaled) with choice outcomes. While this has been true for all suboptimal choice research conducted thus far, it is possible to arrange varying degrees of correlation between TL stimuli and choice outcomes. For example, choice for the suboptimal alternative might produce one of two stimuli: one stimulus signals a 75% chance of food whereas the other stimulus signals a 25% chance of food (or maybe even the more extreme case in which one stimulus signals a 99% chance of food whereas the other signals a 1% chance of food). In this situation, the suboptimal alternative provides two temporally informative signals (rather than one, as we assumed above). Calculating temporal information conveyed by TL stimuli that are arranged on the same alternative is done in the same way as that just described (i.e., Equation 7 would be applied to each TL stimulus that signals a probability of food greater than 0, even if those stimuli are arranged on the same alternative). However, it is not clear how to characterize and quantify how much temporal information is available for an alternative that offers two temporally informative signals when each signal conveys a different amount of temporal information (as would be the case with varying degrees of correlation between TL stimuli and choice outcomes). For example, should one simply average the number of bits of temporal information provided by the two temporally informative signals, or should they be added? Or, is it a winner-take-all competition in which the signal providing less temporal information is completely ignored? It is currently unclear exactly how multiple temporally informative signals interact when they are arranged for the same alternative, but exploring this question is an important step in extending the temporal information-theoretic approach to a wide range of potential suboptimal choice situations that have yet to be examined.

Conclusion

Application of the temporal information-theoretic approach to suboptimal choice formalizes the notion that stimuli influence suboptimal choice through the information they convey about food delivery. Importantly, this approach formalizes the critical role that *temporal* information plays in the ability of stimuli to influence suboptimal choice, rather than information about whether or not food will occur, as others have suggested (e.g., Vasconcelos et al., 2015). We also assume, as have others (Zentall, 2016), that the amount of food signaled by a stimulus contributes to its overall value. Thus, we use the term signal value to summarize the joint influence of temporal information and amount of food on the ability of a food-predictive signal to support choice responses. This temporal information-theoretic approach provides a reasonably accurate characterization of the role stimuli play in suboptimal choice (see Figure 3) and therefore provides a formal, quantitative framework to understand how stimuli influence suboptimal choice in manner that is consistent with the impact food-predictive signals have in other preparations used to study conditioned reinforcement (see Shahan & Cunningham, 2015) as well as Pavlovian conditioning (see Balsam et al., 2010). In order to account for the effects of IL and TL duration on suboptimal choice, we developed a model of suboptimal choice based on (1) relative signal value (i.e., Equation 10), (2) relative primary reinforcement rate (i.e., Equation 11), and (3) competition between relative signal value and relative primary reinforcement rate that is governed by the relative temporal proximity of informative signals and food at the choice point (i.e., Equations 12 and 13). Based on the reanalysis presented in Figure 5, this model provides a reasonable description of suboptimal choice and might be considered a first attempt at a working quantitative model of suboptimal choice based on temporal information.

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Appendix A

Cycle time in a concurrent chains procedure, in which the suboptimal and optimal schedules of reinforcement operant concurrently, is calculated slightly differently than a discrete trial procedure. Consider a procedure in which pigeons choose between signaled 50% reinforcement (the suboptimal alternative) and 100% reinforcement (the optimal alternative). Initial-link duration is 60 s while terminal link duration is 10 s. Because the two IL schedules operate concurrently, mean time to transition to a TL is half the IL schedule value, thus 30 s. Further, because the suboptimal TL is entered half the time and the optimal TL is entered the other half, mean time spent in the TL is the average of the TL durations for the two alternatives. The overall average inter-outcome interval is therefore [30 s + .5(10 s + 10 s)] = 40 s. The probability that this outcome ends in food is p=0.5 half of the time (for the suboptimal alternative) and p=1 the other half of the time (for the optimal alternative). Thus, the overall average time to food (i.e., cycle time), is 40 s/[(.5 X .5) + (.5 X 1)] = 53.3 s. This formulation can be generally represented as

$$C = \frac{(.5\,IL) + .5\left(TL_{sub} + TL_{opt}\right)}{(.5\,pSr_{sub}) + \left(.5\,pSr_{opt}\right)}$$

where IL and TL are initial-link and terminal-link duration, respectively, and *pSr* is reinforcement probability. This equation can be used to calculate cycle time in a concurrent chains suboptimal choice procedure (see also Spetch & Dunn, 1987 for a description of how to calculate overall average time to food in a suboptimal concurrent chains procedure). Trial time is calculated as in Equation 7 in the main text.

Appendix B

Here we illustrate why IL and TL durations influence relative temporal informativeness in standard concurrent-chains schedules but not in the suboptimal choice research employing concurrent chains described in the main text (e.g., Dunn & Spetch, 1990; Kendall, 1985; Spetch et al., 1990; Spetch et al., 1994). It is of critical importance to note that when IL and TL durations are manipulated in standard concurrent-chains schedules, there is a difference in delay to food signaled by TL stimuli (i.e., *t*) between alternatives. For example, the delay to food signaled by the TL stimulus for alternative one might be t_1 = 2 s whereas the delay to food signaled by the TL stimulus for alternative two might be t_2 = 4 s. Thus, TL_1 signals half the wait time to food as TL_2 and is therefore more temporally informative. However, the *degree* to which this is true depends on the absolute value of *C*/*t* for each TL stimulus. Consider the case in which concurrent VI 6 s schedules are used in the ILs, with TL_1 = 2 s and TL_2 = 4 s. Using Appendix A to calculate *C* and Equation 7 to calculate *t*, *C*/*t* for TL_1 is 6 s / 2 s = 3, whereas *C*/*t* for TL_2 is 6 s / 4 s = 1.5. Thus, *C*/*t* for TL_1 is twice that for TL_2. Converting *C*/*t* into temporal information, TL_1 conveys 1.6 bits of temporal information whereas TL_2 conveys .58 bits of temporal information, making the ratio of temporal information conveyed by TL_1 and TL_2 equal to H_1 / H_2 = 2.7 (i.e., TL_1 is almost three times as informative as TL_2).

Now consider what happens when IL duration is increased to concurrent VI 120 s schedules. Increasing the IL VI schedule increases *C* but does not change *t* for either alternative. Thus, *C*/*t* associated with each TL stimulus will increase. Specifically, *C*/*t* for TL_1 becomes 63 s / 2 s = 31.5, while *C*/*t* for TL_2 becomes 63 s / 4 s = 15.75. Converting

C/*t* to bits, H_1 = 5.0 whereas H_2 = 4.0. While *C*/*t* associated with TL_1 is still twice that of TL_2, the ratio of their *temporal informativeness* is now dampened because of the logarithmic nature of the conversion to bits, with H_1 / H_2 = 1.25 following the increase in IL duration. Thus, increasing IL duration decreases relative temporal informativeness from 2.7 to 1.25.

Consider now what happens when TL duration for each alternative is increased. We start with VI 120 s IL schedules with TL_1 = 2 s and TL_2 = 4 s (i.e., the same schedule values as the long-IL example above). Remember that relative temporal informativness under these conditions is H_1 / H_2 = 1.25. IL schedules remain constant at VI 120 s but we increase TL_1 to 40 s and TL_2 to 80 s (maintaining the two-fold difference in *t* between TL stimuli). Increasing TL duration increases both *C* and *t* for each alternative, but overall produces a decrease in *C*/*t* for each alternative (because *t* increases to a larger degree than *C* when TL duration is increased). As a result, *C*/*t* for TL_1 becomes 120 s / 40 s = 3, while *C*/*t* for TL_2 becomes 120 s / 80 s = 1.5 (again note that *C*/*t* for TL_1 is twice that for TL_2). Converting *C*/*t* into temporal information, H_1 = 1.6 whereas H_2 = .58. Thus, increasing TL duration results in an increase in relative temporal informativeness from H_1 / H_2 = 1.25 (i.e., with the shorter TLs) to H_1 / H_2 = 2.7 (i.e., with the longer TLs).

The question is, why does the above not apply to IL and TL effects in the suboptimal choice research examined in the main text? The answer is that when each TL stimulus is associated with the same *t,* as in suboptimal choice research exploring IL and TL effects, each TL stimulus will have the same *C*/*t*, and therefore convey the same amount of temporal information. Thus, there is no difference in temporal information between TL stimuli to be enhanced or dampened as a result of the logarithmic transformation from *C*/*t* to bits. To illustrate, consider the suboptimal choice procedure in which the suboptimal alternative provides food 50% of the time whereas the optimal alternative provides food 100% of the time (e.g., McDevitt et al., 1997; Spetch et al., 1990; Spetch et al., 1994). The suboptimal alternative provides TL stimuli that differentially signal whether or not food will be delivered while the optimal alternative provides a TL stimulus that is always followed by food. In this preparation there are two temporally informative stimuli, the food-predictive TL stimulus for the suboptimal alternative and the TL stimulus for the optimal alternative.

First, consider what happens to relative temporal informativeness when IL duration is increased. Let us assume that TL duration for each alternative is 10 s, and that IL duration is increased from concurrent VI 10 s to concurrent VI 90 s. Regardless of IL duration, the TL stimulus associated with food for both suboptimal and optimal alternatives is 10 s (because each stimulus is followed by food 100% of the time – see Equation 7). When VI 10 s IL schedules are used, *C*/*t* for both TL stimuli is 15 s / 10 s = 1.5. Thus, each TL stimulus conveys .58 bits of temporal information. When IL schedules increase to VI 90 s, *C*/*t* for each alternative increases to 55 s / 10 s = 5.5, thereby conveying 2.5 bits of temporal information. However, note that relative temporal informativeness (H_{sub} / H_{opt}) is 1 in both cases. Thus, increasing IL duration does not influence relative temporal informativeness, and indeed cannot do so when each TL stimulus is associated with the same *C*/*t*.

Now consider what happens when TL duration is increased. Let us assume VI 90 s IL schedules with an increase in TL duration from 10 s to 90 s. As before, VI 90 s IL schedules and 10 s TL durations results in a *C*/*t* of 55 s / 10 s = 5.5 for each alternative, and therefore each TL stimulus convey 2.5 bits of temporal information. When TL duration is increased, both *C* and *t* increase, but overall *C*/*t* decreases for each TL stimulus (again because *t* is increased to a greater degree than *C* when TL duration is increased). With 90 s TL durations, *C*/*t* for each alternative is 135 s / 90 s = 1.5, and therefore TL stimuli for both suboptimal and optimal alternatives convey .58 bits of temporal information. Again, H_{sub} / H_{opt} = 1 for both 10 s and 90 s TL durations, and indeed will always be 1 regardless of TL duration.

Appendix C

As noted in the body of the text, Shahan & Cunningham (2015) demonstrated that relative temporal informativeness (i.e., H1/H2) changed in a manner similar to relative conditioned reinforcing value in Delay Reduction Theory (i.e., DRT) when applied to three ubiquitous findings in concurrent-chains research (i.e., increasing preference for a TL stimulus with increasing relative reinforcement in the presence of that stimulus, the initial-link effect, and the terminal link effect). The expansions proposed in Equations 12 and 13 do not negatively affect the temporal information-theoretic model's ability to account for these effects, but instead augments Shahan & Cunningham's analysis by providing a means to convert relative temporal informativeness into behavioral output.

With respect to the three effects described above, most models of concurrent-chains performance make nearly identical predictions. Thus, for simplicity, we shall compare the predictions of the current model to the Squires & Fantino (1971) version of DRT which suggests that:

$$\frac{B_1}{B_1+B_2}=\frac{R_1(C-t_1)}{R_1(C-t_1)+R_2(C-t_2)} \qquad \text{(A1)},$$

where *B* refers to the number of responses for an alternative (identified by the subscript), *R* refers to the rate of primary reinforcement for an alternative, *C* refers to the overall average time to food, and *t* refers to the average time to food following TL onset for an alternative. The term in the parenthesis (i.e., $C - t$) defines conditioned-reinforcing value within the framework of DRT and specifies that value depends on the degree to which TL onset is associated with a reduction in delay to food (i.e., t) relative to the overall delay to food (i.e., *C*).

The temporal information-theoretic model is defined by Equations 12 and 13 and can be found in the main text. We set all sensitivity parameters in the temporal information-theoretic model to 1 (i.e., a and b) and set parameter values for m and β to 1 and 2, respectively. We generated behavioral predictions from both DRT (Equation A1 above) and the temporal information-theoretic model under conditions in which relative reinforcement rate in the TL, absolute IL duration, and absolute TL duration vary. As is customary in concurrent-chains research, we assume that variable interval (VI) schedules are used in both the IL and TL. Below we describe IL and TL schedule values used to generate predictions.

Relative reinforcement rate in the TLs. We assume concurrent VI 60 s schedules in the ILs. The ratio of reinforcement rates provided by the terminal links was assumed to vary while the overall average rate of reinforcement provided by the TLs was held constant at 1/30 s. Three pairs of TL schedules were examined using the following VI schedules for TL_1 / TL_2: VI30s/VI30s (i.e., 1/1), VI20s/VI40s (i.e., 2/1), and VI12s/VI48s (i.e., 4/1).

IL Effect. TL_1 signaled a VI 10 s schedule whereas TL_2 signaled a VI 30 s schedule. Thus, the rate of primary reinforcement signaled by TL_1 was always three times that signaled by TL_2. IL durations increased using concurrent VI 40-s, VI 120-s, and VI 600-s schedules.

TL Effect. Concurrent VI 300 s schedules operated in the ILs while the rate of reinforcement signaled by TL_1 was always three times that signaled by TL_2. However, overall TL duration increased using the following VI schedules for TL_1 / TL_2: VI 10s/VI30s; VI 30s/VI 90s; VI 90s/VI 270s.

As shown in Figure A1, the temporal-information-theoretic model described in the main text generates behavioral predictions very similar to those generated by DRT (and will therefore generate very similar predictions to other models of concurrent-chains). Thus, the expansion of the temporal information-theoretic model proposed here for suboptimal choice (i.e., Equations 12 and 13) can also serve as a theory of concurrent-chains performance and conditioned reinforcement more generally.

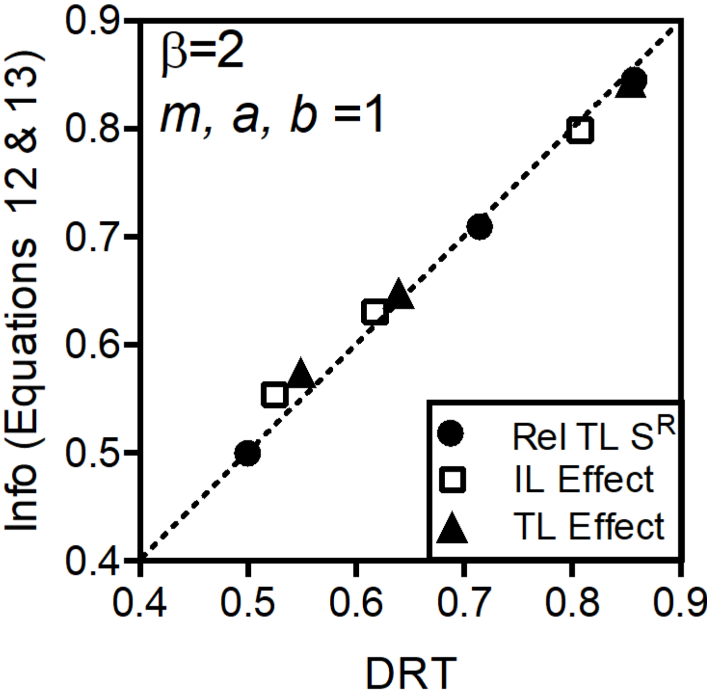
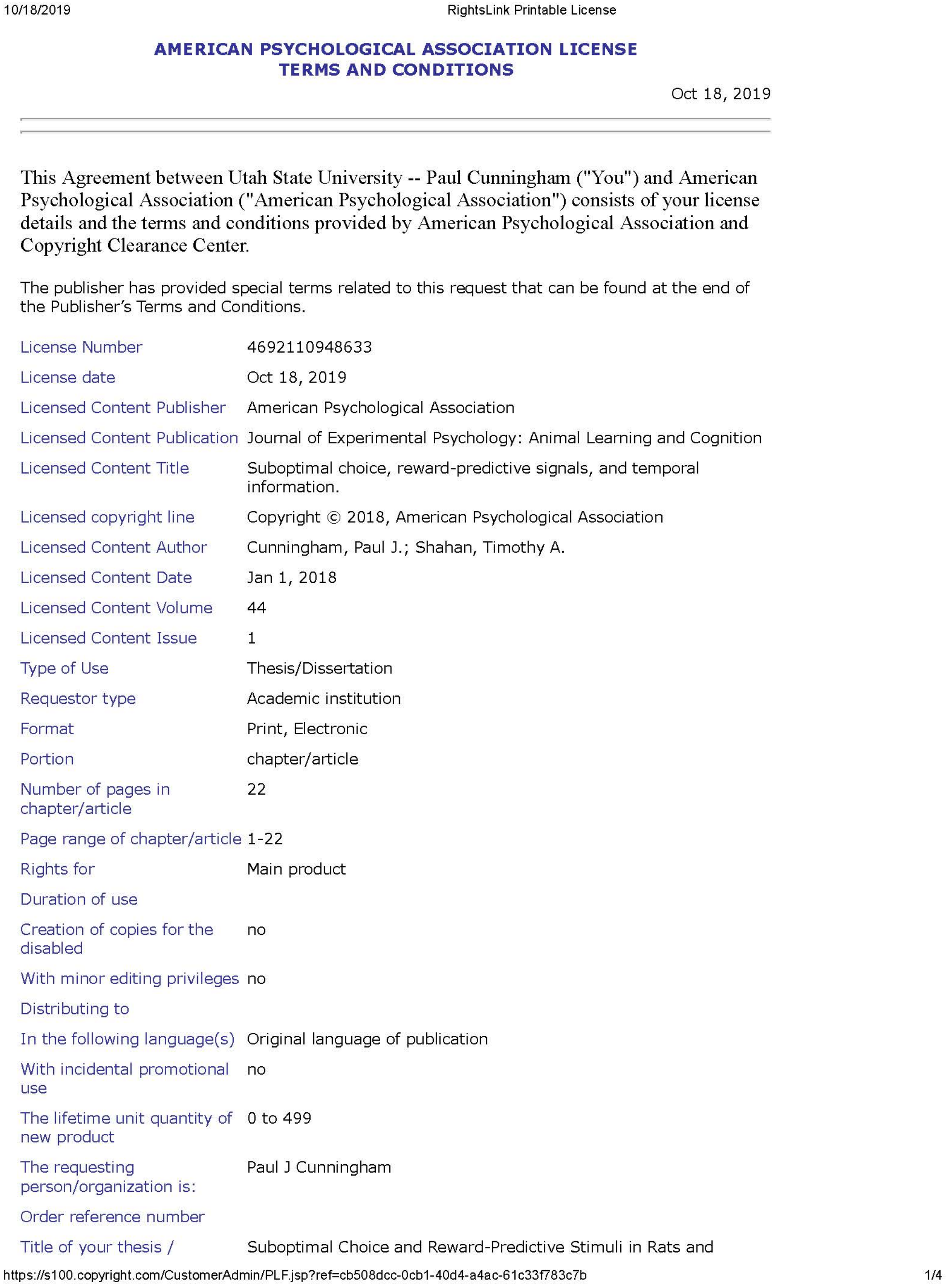


Figure A1. The y-axis depicts predicted choice proportions for three ubiquitous findings within the concurrent chains choice literature generated by the temporal information-theoretic model (Equations 12 & 13). The x-axis shows the same predictions generated by Delay Reduction Theory (Equation A1).

Appendix D



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CHAPTER 3

Rats Engage in Suboptimal Choice When the Delay to Food is Sufficiently Long[9]

Abstract

Numerous examples in the decision-making literature demonstrate that animals sometimes make choices that are not in their long-term best interest. One particular example finds pigeons preferring a low-probability alternative in lieu of a high-probability alternative, referred to as suboptimal choice. While there is ample evidence that pigeons engage in such suboptimal choice, there is currently weak evidence (at best) that rats also do so. Cunningham & Shahan's (2018) temporal information-theoretic model suggests that suboptimal choice in pigeons arises when 1) the low-probability alternative provides stimuli that convey more temporal information than stimuli associated with the high-probability alternative, and 2) when the delay to food is much longer relative to the delay to temporally informative signals at the choice point. The latter condition plays the important role of biasing decision-making to be governed by the relative temporal information conveyed by stimuli rather than the relative rate of food delivery. The present experiment explored the possibility that rats will engage in suboptimal choice if the delay to food at the choice point is sufficiently long, as the temporal information-theoretic model suggests. Rats were given a choice between a suboptimal alternative providing food 20% of the time and an optimal alternative

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providing food 50% of the time. The suboptimal alternative provided stimuli that differentially signaled choice outcomes whereas the optimal alternative did not. The post-choice delay was manipulated across conditions and ranged from 10 s to 50 s. As with previous research, rats did not engage in suboptimal choice when the post-choice delay was 10 s. However, once the delay was at least 30 s, rats engaged in suboptimal choice. These results are consistent with the temporal information-theoretic model of suboptimal choice and suggest that rats and pigeons likely do not differ in the decision-making processes involved in the suboptimal choice procedure.

Key words: Suboptimal Choice, Rats, Temporal Information, Conditioned Reinforcement, Information Theory

Introduction

Normative accounts of decision-making suggest that animals ought to make decisions in their long-term best interest. For example, Optimal Foraging Theory (Stephens & Krebs, 1986) suggests that evolution has sculpted decision-making mechanisms that maximize a forager's net energy gain. However, there are numerous examples of animals making decisions that are not in their long-term best interest (e.g., by making decisions that reduce their overall rate of food delivery) which often provide important insights into decision-making processes in animals. When viewed in the context of normative accounts of decision-making, examples of maladaptive decision-making raise questions about how decision-making mechanisms are adapted to problems encountered in an animal's natural environment and how these decision-making mechanisms can lead to maladaptive outcomes in unnatural laboratory situations (e.g., Stephens & Anderson, 2001; Vasconcelos, Montiero, & Kacelnik, 2015).

Figure 1 illustrates a choice procedure that has been used to study one form of maladaptive decision-making in pigeons. Specifically, pigeons are given a choice between two response keys in an initial-link (IL) choice phase. A single choice response in the IL initiates a delay, referred to as the terminal-link (TL), which ends probabilistically with food. One alternative, the suboptimal alternative, provides a low probability of food (e.g., $p = 0.2$) while also providing TL stimuli that differentially signal the choice outcome (i.e., TL stimuli are correlated with food delivery). The other, optimal, alternative provides a higher probability of food (e.g., $p = 0.5$) but does not provide TL stimuli that differentially signal food (i.e., the TL stimuli are uncorrelated with food delivery). Although the optimal alternative offers more food in the long-run, pigeons often prefer the suboptimal alternative (see Zentall, 2016 for review). For this reason, preference for the suboptimal alternative is referred to as suboptimal choice.

Extensive research has demonstrated that suboptimal choice arises because the suboptimal alternative provides a TL stimulus that is a perfect predictor of food (i.e., the food-predictive stimulus that is always followed by food; the S+) whereas the optimal alternative provides TL stimuli that are less reliable predictors of food (i.e., optimal TL stimuli are only sometimes followed by food). In this way, pigeons are willing to sacrifice food in order to earn food-predictive stimuli (i.e., animals are willing to sacrifice food for information about food – Vasconcelos et al., 2015). As a result, many have suggested that suboptimal choice is governed by the conditioned-reinforcing properties of TL stimuli, acquired through their predictive (or informative) relation to food (Cunningham & Shahan, 2018; McDevitt et al., 2016; Zentall, 2016). Thus, exploring the decision-making processes that give rise to suboptimal choice in pigeons can reveal

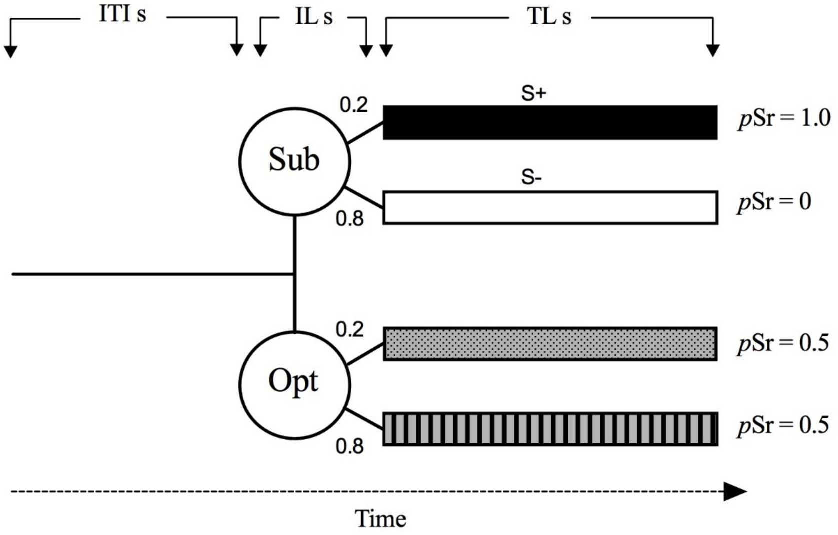

Figure 1. Depiction of the suboptimal choice procedure in which the suboptimal alternative provides TL stimuli that differentially signal food while the optimal alternative does not.

insights into the manner in which reward-predictive stimuli contribute to maladaptive decision-making.

Further, some have suggested that the decision-making processes that give rise to suboptimal choice in pigeons play a role in human gambling disorders (e.g., Zentall, 2014). It is argued that the stimuli accompanying a winning pull on a slot machine (i.e., the stimuli that predict money) entice individuals to continue gambling even though they ultimately lose money for doing so, much like food-predictive stimuli entice pigeons to choose an alternative that offers less food in the long-run. Indeed, Molet et al., (2014) found that more frequent gamblers exhibit a greater degree of suboptimal choice than less frequent gamblers in a human-variant of the suboptimal choice procedure. Thus, the study of suboptimal choice in pigeons might reveal important insights about evolutionarily conserved, species-general decision-making processes that contribute to clinically relevant behavioral disorders like problematic gambling.

However, the species-generality of the decision-making processes that govern suboptimal choice has been questioned because rats do not appear to engage in suboptimal choice in procedures like those used with pigeons. Trujano & Orduña (2015) gave rats a choice between a suboptimal alternative providing food 20% of the time with TL stimuli differentially signaling food and an optimal alternative providing food 50% of the time without TL stimuli differentially signaling food (TL stimuli consisted of small LED lights). Rats, unlike pigeons, preferred the optimal alternative under these conditions (see also Ojeda, Murphy, & Kacelnik, 2018; Trujano, López, Rojas-Leguizamón, & Orduña, 2016).

Chow et al., (2017) suggested that TL stimuli need to acquire incentive salience (i.e., elicit sign-tracking responses – Robinson & Berridge, 1993) for rats to engage in suboptimal choice. For this reason, rats should engage in suboptimal choice when levers (but not lights) are used as TL stimuli given extensive research showing that rats typically sign-track small, manipulable objects that predict food (i.e., levers). Chow et al., explored this possibility by comparing suboptimal choice in rats with either levers or lights as TL stimuli. Rats were first given a choice between two alternatives, each providing a 50% chance of food, with one alternative providing differential TL stimuli and the other alternative without differential TL stimuli. Once preference for the differential TL stimuli was established (without cost), the chance of food for that alternative was reduced to 25% and then 12.5% across conditions, thereby making this alternative suboptimal. Chow et al., found that rats with levers, but not lights, as TL stimuli continued to prefer the differential TL stimuli (though to a lesser degree) even when that alternative became suboptimal via reductions in the probability of food. These results suggested that rats are more likely to engage in suboptimal choice when TL stimuli acquire incentive salience (i.e., maintain sign-tracking). However, it is important to note that Chow et al., (2017) did not find *acquisition* of suboptimal choice in rats. Numerous experiments have subsequently failed to find acquisition of suboptimal choice in rats when levers were used as TL stimuli (Alba et al., 2018; Lopez et al., 2017; Martinez et al., 2017). Thus, the current body of evidence suggests that rats do not engage in suboptimal choice even when TL stimuli acquire incentive salience and elicit sign-tracking (as when levers are used for TL stimuli).

Failures to find suboptimal choice in rats suggests that the decision-making processes that govern suboptimal choice in pigeons might not bear relevance to decision-making processes in mammals. Thus, an important issue in suboptimal choice research concerns potential differences in the decision-making processes deployed in the suboptimal choice procedure between rats and pigeons. This issue has implications for the conceptual importance of suboptimal choice (i.e., the degree to which the study of suboptimal choice reveals insights into species-general decision-making processes) as well as its potential clinical significance (i.e., the degree to which the study of suboptimal choice can reveal insights into problematic gambling in humans).

Numerous frameworks have been developed in attempts to understand suboptimal choice. Some of these frameworks are designed to understand the adaptive value of decision-making processes that lead to suboptimal choice in unnatural laboratory situations but lead to more optimal outcomes in the animal's natural environment (e.g., Vasconcelos et al., 2015; Vasconcelos, Machado, & Pandeirada, 2018). Others are designed to describe how the various consequences associated with suboptimal and optimal alternatives, such as the conditioned-reinforcing value of TL stimuli and the parameters of food delivery, interact to encourage suboptimal choice (e.g., Cunningham & Shahan, 2018; Daniels & Sanabria, 2018; McDevitt, Dunn, Spetch, & Ludvig, 2016; Zentall, 2016). In this paper we use Cunningham & Shahan's (2018) temporal information-theoretic model of suboptimal choice to explore the conditions under which rats might engage in suboptimal choice. The temporal information-theoretic model quantitatively describes 1) the manner in which TL stimuli influence choice, 2) the manner in which reinforcement rate influences choice, and 3) how TL stimuli and reinforcement rate compete to control choice (as outlined below). The temporal information-theoretic model accounts for a vast majority of suboptimal choice research in pigeons (see Cunningham & Shahan, 2018) and provides a quantitative framework to study and understand potential differences and similarities in suboptimal choice between rats and pigeons.

The first component of the temporal information-theoretic model describes the impact of TL stimuli on choice. According to the temporal information-theoretic model, TL stimuli influence choice according to the relative temporal information they convey (i.e., the information conveyed by TL stimuli about *when* to expect food). Specifically, TL stimuli influence choice based on the choice rule:

$$\frac{H_{sub}^{a}}{H_{sub}^{a}+H_{opt}^{a}} \qquad (1),$$

where H refers to the bits of temporal information conveyed by TL stimuli for each alternative (identified by subscript) and *a* refers to the sensitivity of choice to relative temporal information. Equation 1 states that pigeons prefer the alternative that provides the more temporally informative TL stimulus. The notion that temporal information governs the ability of stimuli to function as conditioned reinforcers stems from 1) successful applications of the temporal information-theoretic approach to Pavlovian Conditioning (Balsam et al., 2010), and 2) the notion that Pavlovian conditioning governs the ability of stimuli to function as conditioned reinforcers (see Shahan & Cunningham, 2015; Shahan, 2017). Thus, the temporal information-theoretic approach offers a unified, quantitative framework to understand both Pavlovian conditioning and conditioned reinforcement. Further, Cunningham & Shahan (2018) assume that the TL stimulus never followed by food (i.e., the S-) does not influence choice (see Fortes, Vasconcelos, & Machado, 2016 for strong evidence suggesting pigeons indeed ignore the S-).

Because choice responses produce both temporally informative stimuli *and* food itself, the temporal information theoretic model assumes that relative reinforcement (food) rate also influences choice, according to the generalized matching law:

$$\frac{R_{sub}^{b}}{R_{sub}^{b}+R_{opt}^{b}} \qquad (2),$$

where R refers to reinforcement rate and *b* refers to the sensitivity of choice to relative reinforcement rate (Baum, 1974). The impact of relative reinforcement rate on choice describes the second component of the model and suggests that relative temporal information and relative reinforcement rate compete to control choice. This competition is captured by the equation:

$$pSub = w\frac{H_{sub}^{a}}{H_{sub}^{a}+H_{opt}^{a}} + (1-w)\frac{R_{sub}^{b}}{R_{sub}^{b}+R_{opt}^{b}} \qquad (3),$$

where *w* is a weighting mechanism that determines the degree to which choice is governed by relative temporal information and relative reinforcement rate. When *w* is close to 1, choice is governed largely by relative temporal information and pigeons should prefer the alternative providing the more temporally informative TL stimulus. When *w* is close to 0, choice is governed largely by relative reinforcement rate and pigeons should prefer the alternative providing the higher rate of reinforcement. When TL stimuli differentially signal choice outcomes for the suboptimal but not optimal alternative (as in Figure 1), the food-predictive TL stimulus for the suboptimal alternative (i.e., the S+) conveys more temporal information than TL stimuli for the optimal alternative. In this way, the suboptimal choice procedure pits relative temporal information against relative reinforcement rate such that the alternative providing the lower reinforcement rate also provides the more temporally informative TL stimulus (i.e., the suboptimal alternative; see Cunningham & Shahan, 2018 for thorough explanation). Thus, according to the temporal information-theoretic model, any manipulation that increases *w* will increase preference for the suboptimal alternative.

The third component of the model describes the variables that govern the weighting mechanism (i.e., *w*). Specifically, the weighting mechanism is governed by the average delay to food relative to the average delay to the temporally informative signals at the choice point (defined by the moment at which the choice responses are presented), as described by the logistic function:

$$w = \frac{1}{1+e^{-\beta\left(\frac{D_f}{D_s}-m\right)}} \qquad (4).$$

D_f represents the average delay to food (regardless of which alternative it came from) whereas D_s represents the average delay to temporally informative signals (regardless of which alternative it came from) at the choice point, β represents the sensitivity of w to variations in D_f/D_s, and m represents a bias *against* using the relative temporal information conveyed by signals to make decisions (specifically, m indicates the value of D_f/D_s at which w is 0.5). According to Equation 4, when there is a longer delay to food relative to temporally informative signals at the choice point (i.e., as D_f/D_s approaches ∞), w approaches 1 and choice should be governed by the relative temporal information provided by signals and, as a result, suboptimal choice should emerge.

The weighting mechanism portrayed in Equation 4 was designed to describe the effects of IL and TL duration on suboptimal choice in pigeons (Cunningham & Shahan, 2018; McDevitt et al., 2016). Specifically, incorporating Equation 4 into Equation 3 accounts for the fact that suboptimal choice in pigeons emerges only with a short IL duration (e.g., a fixed-ratio 1 IL schedule) *and* a long TL duration (e.g., 10 s). Short IL durations result in relatively short delays to temporally informative signals at the choice point (i.e., a small value of D_s) while long TL durations result in relatively long delays to food at the choice point (i.e., a large value of D_f). Thus, with short IL durations and long TL durations, the value of D_f/D_s will be relatively large, indicating that temporally informative signals are much closer in time than food itself at the choice point. This, in turn, increases the weight given to temporally informative signals (via *w*) and therefore encourages suboptimal choice when the suboptimal, food-predictive TL stimulus (S+) conveys more temporal information than optimal TL stimuli, though the degree to which it does so depends on the parameter values for *m* and *β*.

Within this temporal information-theoretic framework, it is possible that the reason previous experiments failed to find suboptimal choice in rats is that the value of D_f/D_s was not large enough to increase *w*. A large majority of previous experiments exploring suboptimal choice in rats have used a fixed-ratio (FR) 1 IL schedule with a 10 s TL duration. This is perhaps not surprising because these values are sufficient to produce suboptimal choice in pigeons. However, evidence from the inter-temporal choice literature suggests that rats might require longer delays to food than pigeons before making maladaptive choices. Specifically, when rats and pigeons are given a choice between a small amount of food delivered immediately and a larger amount of food delivered after a delay, rats are willing to tolerate longer delays to receive the larger food than pigeons before switching preference to the maladaptive alternative offering the smaller, immediate food (Green et al., 2004; Mazur, 2000; Mazur & Biondi, 2009; Tobin

& Logue, 1994). Thus, rats are willing to tolerate longer delays to food than pigeons before engaging in maladaptive choice. Perhaps the delay to food, as determined primarily by TL duration in the suboptimal choice procedure, needs to be longer for rats than pigeons for suboptimal choice to emerge. Indeed, Laude et al., (2014) found that more impulsive pigeons (as measured by sensitivity of choice to delayed food) were more likely to engage in suboptimal choice than less impulsive pigeons, further suggesting the possibility that suboptimal choice depends in part on sensitivity to delayed food delivery.

The only study that has used a TL duration longer than 10 s in rats comes from Trujano & Orduña (2015), who found no statistical difference in suboptimal choice between 10 s and 30 s TL durations (though there was a slight trend towards more suboptimal choice with a 30 s TL duration). Nevertheless, there are currently no studies systematically exploring the effect of TL duration on suboptimal choice in rats across a wide range of TL durations, despite numerous experiments demonstrating more suboptimal choice with longer TL durations in pigeons (e.g., Kendall, 1984; McDevitt, Pisklak, Spetch, & Dunn, 2018; Spetch et al., 1990; Spetch et al., 1990). Thus, the present experiment examined the effect of TL duration on suboptimal choice in rats. According to the temporal information-theoretic model, longer TL durations increase the delay to food at the choice point and therefore increases the value of D_f/D_s. As a result, the weight given to relative temporal information as a determinant of choice should increase and suboptimal choice should become more likely with longer TL durations.

Methods

Subjects. Ten male Long-Evans rats (Charles River, Portage, MI), approximately 240 days old at the start of the experiment, served as subjects. Rats were individually housed in a temperature-controlled colony room with a 12:12 light/dark cycle. Rats were maintained at 80% of their free-feeding weight and had free access to water in their home cages. All rats had previous experience with lever-pressing for food under variable-interval schedules reinforcement and extinction. They did not have previous experience with the suboptimal choice procedure (or any other decision-making paradigm). Animal housing and care, and all procedures used, were conducted in accordance with Utah State University's Institutional Animal Care and Use Committee.

Apparatus. Ten identical modular operant chambers (Med Associates, St. Albans, VT), each housed in a sound-attenuating cubicle, were used. Each chamber was constructed of clear Plexiglas with aluminum work panels on the front and back walls. Near the bottom on the center panel of the front wall was a feeder aperture into which 45 mg grain-based food pellets (Bio Serv, Flemington, NJ) were delivered. Pellet deliveries were accompanied by 3-sec feeder illumination with a 28 vdc feeder light. Two retractable levers with stimulus lights above each were located equidistant from the feeder aperture to the left and right of the center panel. A 28 vdc houselight was located at the top of the center panel on the front wall of the chamber. Finally, a tone-generator was located in the upper-left corner of the front panel.

Procedure. Prior to the suboptimal choice procedure, all rats received 5 sessions of lever-press training in which a single lever, either left or right, was inserted into the chamber on a pseudo-random basis, with the constraint that neither lever could be presented more than twice in a row. A single lever press immediately delivered food, after which a 10 s inter-trial interval (ITI) ensued. Following the 10 s ITI, the next trial began. Each lever was presented 15 times per session. The purpose of this training was to ensure that rats pressed each lever with approximately the same latency before the experiment proper began.

The suboptimal choice procedure consisted of a choice between a suboptimal alternative delivering food 20% of the time and an optimal alternative delivering food 50% of the time, with choice alternatives defined by left and right levers (assignment counterbalanced across subjects). The probability of food was determined by querying a probability gate when a choice lever was pressed (with a constant probability across trials). A single choice response in the initial-link (IL) resulted in a transition to the terminal-link (TL) whose duration varied across conditions (detailed below). The suboptimal alternative provided TL stimuli that differentially signaled food whereas the optimal alternative provided a TL stimulus that did not differentially signal food. The food-predictive TL stimulus for the suboptimal alternative and the TL stimulus for the optimal alternative consisted of a constant or flashing (1 flash/sec) stimulus-light + tone compound (counterbalanced across subjects). For example, the food-predictive TL stimulus for the suboptimal alternative (i.e., the S+) might consist of a *flashing* stimulus-light + tone compound whereas the TL stimulus for the optimal alternative would consist of a *constant* stimulus-light + tone compound, with the stimulus light located above the lever defining a given alternative. Note that only a single TL stimulus was used for the optimal alternative. A blackout was used for the TL stimulus never followed by food (i.e., S-) for the suboptimal alternative. Alba et al., (2018) found that neither the stimulus-modality of the S- (i.e., lever vs. blackout) nor the number of TL stimuli for the optimal alternative (i.e., one vs. two TL stimuli) affects suboptimal choice in rats.

Each session consisted of 48 forced-exposure trials and 24 free-choice trials. Trial-types were randomly presented in blocks of three such that every three trials consisted of two forced-exposure trials (one for each alternative) and one free-choice trial. Each trial began with illumination of the houselight, which signaled that the rat must make a centering response into the feeder. During forced-exposure trials, either the optimal or suboptimal lever was extended into the chamber following the centering response. A single lever press turned off the houselight, retracted the lever, and resulted in a transition to the TL. A lever press during optimal forced-exposure trials resulted in presentation of the TL stimulus, with a 50% chance of the TL ending with a single food pellet and a 50% chance of the TL ending with a 3 s blackout. During suboptimal forced exposure trials, a lever press resulted in the food-predictive TL stimulus (S+) 20% of the time and a blackout (S-) 80% of the time. The food-predictive TL stimulus was always followed by delivery of a single food pellet and the blackout was never followed by food. Free-choice trials were the same as forced-exposure trials with the exception that both suboptimal and optimal levers were extended into the chamber. Each trial was separated by a 10 s ITI.

TL duration varied from 10 s to 50 s across conditions for each rat. For half of the rats, TL durations were presented in the following order: 10 s, 50 s, 20 s, 40 s, then 30 s. The sequence of TL durations for the other half of rats was: 50 s, 10 s, 40 s, 20 s, then 30 s[10]. Once the last TL-duration condition was completed, each rat received the first TL duration they experienced in order to assess potential history effects. Each TL-duration

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[10] Rats K21, K22, K25, K26, and K29 received the 50 s, 10 s, 40 s, 20 s, then 30 s TL duration sequence. Rats K23, K24, K27, K28, and K30 received the 10 s, 50 s, 20 s, 40 s, then 30 s TL duration sequence.

condition lasted at least 30 sessions and until the group mean was stable, which was determined using visual inspection[11]. The primary dependent measure was the proportion of choices made to the suboptimal alternative (i.e., suboptimal responses/total responses). The rate of responding in the food hopper during each TL stimulus was also recorded and analyzed.

Results

Figure 2 depicts mean rate of responding in the feeder during each of the three TL stimuli, averaged from the last 5 sessions of each condition. The purpose of this analysis was to ensure that rats discriminated TL stimuli and learned the relation between TL stimuli and food delivery. A 3 X 5 (TL stimulus x TL duration) repeated measures analysis of variance (ANOVA) revealed a significant main effect of TL stimulus, $F(2,18) = 66.3$, $p < .001$, a significant main effect of TL duration, $F(4,26) = 12.4$, $p < .001$, and a significant TL stimulus by TL duration interaction, $F(8,72) = 6.2$, $p < .001$. Several pairwise comparisons were conducted to determine the source of the interaction. These analyses revealed that responding was higher in the suboptimal S+ than the S-, but this difference decreased as TL duration increased, $F(4,36) = 5.8$, $p < .001$. Further, responding was higher in the optimal TL stimulus than the suboptimal S-, but this difference also decreased as TL duration increased, $F(4,36) = 10.6$, $p < .001$. There was no difference in responding between the suboptimal S+ and the optimal TL stimulus, $F(4,36) = 1.4$, $p = .266$. Thus, rats readily discriminated stimuli predictive of food from stimuli that did not predict food, as indicated by more responded in the feeder in the

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[11] The only condition lasting longer than 30 sessions was the second TL duration presented to the rats. All other TL-duration conditions lasted 30 sessions.

presence of the suboptimal S+ and the optimal TL stimulus than in the presence of the suboptimal S-. Further, responding in the presence of the suboptimal S+ and the optimal TL stimulus decreased as TL duration increased.

Figure 3 depicts mean suboptimal choice, averaged across the last 5 sessions of each condition, as a function of TL duration for each rat. Suboptimal choice increased with TL duration in nine of 10 rats, with K30 being the only rat who preferred the optimal alternative across all TL durations. One-sample t-tests were conducted to determine the shortest TL duration at which suboptimal choice was significantly greater than 0.5 (i.e., indifference) for each rat. Each t-test compared mean suboptimal choice from the last 5 sessions of each condition to indifference. The only rats to prefer the suboptimal alternative with a 10 s TL duration were K22, $t(4) = 6.22$, $p = .003$, $d = .79$;

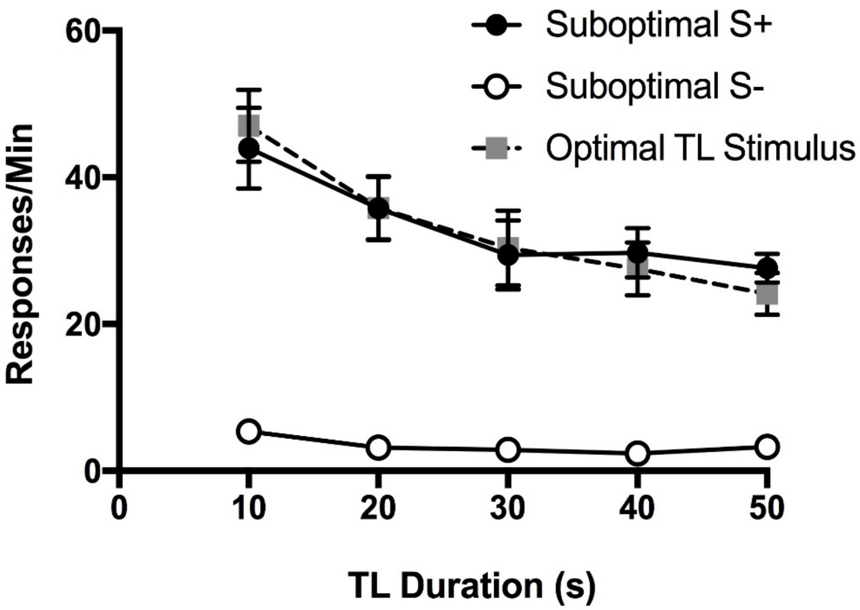

Figure 2. Mean response rate in the presence of the suboptimal S+ (closed circles), the suboptimal S- (open circles), and the optimal TL stimulus (grey squares) as a function of TL duration. Error bars depict standard error of the mean (SEM). Note that SEM for response rate in the S- is obscured by the data point.

and K26, *t*(4) = 5.25, *p* = .006, *d* = .48. Preference for the suboptimal alternative appeared at the 20 s TL duration for K23, *t*(4) = 17.49, *p* < .001, *d* = 1.5. Preference for the suboptimal alternative appeared at the 30 TL duration for K24, *t*(4) = 56.0, *p* < .001, *d* = 1.8; K25, *t*(4) = 9.02, *p* = .001, *d* = .53; K27; *t*(4) = 4.81, *p* = .009, *d* = .92; K28, *t*(4) = 7.67, *p* = .002, *d* = .53; and K29, *t*(4) = 3.17, *p* = .03, *d* = .42. Finally, preference for the suboptimal alternative appeared at the 40 s TL duration for K21, *t*(4) = 7.43, *p* = .002, *d* = .92. Thus, eight of the nine rats to acquire suboptimal choice did so when TL duration was at least 30 s.

To determine potential history effects, a paired-samples t-test was conducted on mean suboptimal choice in the first TL duration condition and the replication condition (with the same TL duration) for each rat. Suboptimal choice was statistically different between the first TL duration condition and the replication condition for six of 10 rats: K21, *t*(4) = 4.81, *p* = .01, *d* = 1.1; K23, *t*(4) = 4.81, *p* = .004, *d* = .14; K24, *t*(4) = 4.81, *p* = .005, *d* = 1.1; K27, *t*(4) = 4.81, *p* = .03, *d* = .02; K29, *t*(4) = 4.81, *p* = .02, *d* = .82; and

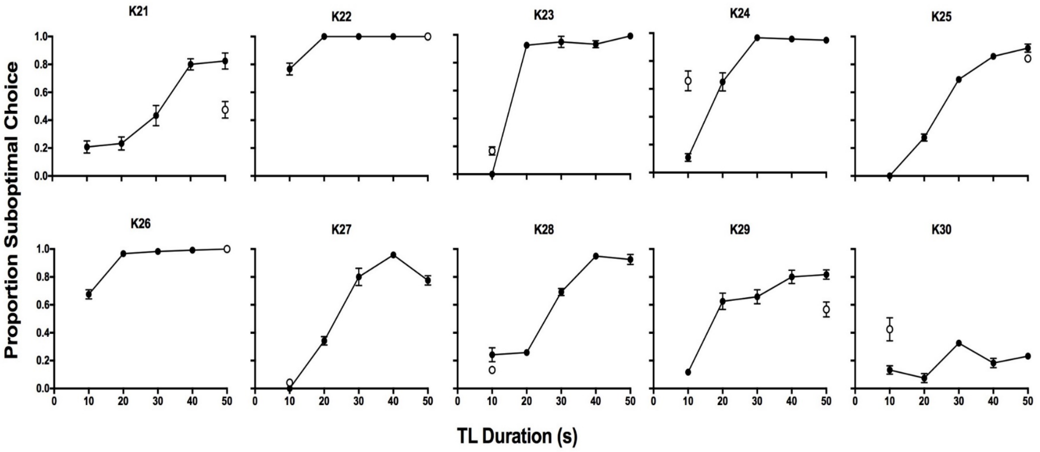

Figure 3. Each panel depicts mean suboptimal choice (averaged from the last 5 days of each condition) for individual subjects as a function of TL duration. The open circle depicts suboptimal choice for the replication condition. Error bars represent SEM.

K30 $t(4) = 4.81$, $p = .05$, $d = .47$. However, the effect size for K23 and K27 was especially small. Thus, while there appear to be some history effects for six of 10 rats, this effect was relatively large for only four rats.

Figure 4 depicts mean suboptimal choice as a function of TL duration. A one-way repeated measures ANOVA revealed a significant effect of TL duration on suboptimal choice, $F(4,36) = 23.5$, $p < .001$. Preference for optimal and suboptimal alternatives across conditions was determined using one-sample t-tests in which mean suboptimal choice was compared to indifference for each TL duration. Suboptimal choice in the 10 s TL duration was statistically below indifference, $t(9) = -3.15$, $p = .012$, $d = .53$, indicating preference for the optimal alternative. Suboptimal choice was statistically greater than indifference for the 30 s TL duration condition, $t(9) = 3.35$, $p = .009$, $d = .73$; the 40 s TL duration condition, $t(9) = 4.46$, $p = .001$, $d = 1.1$; and the 50 s TL duration condition, $t(9) = 4.73$, $p = .001$, $d = 1.1$. Thus, on average, rats preferred the optimal alternative with a 10 s TL duration but preferred the suboptimal alternative once TL duration was at least

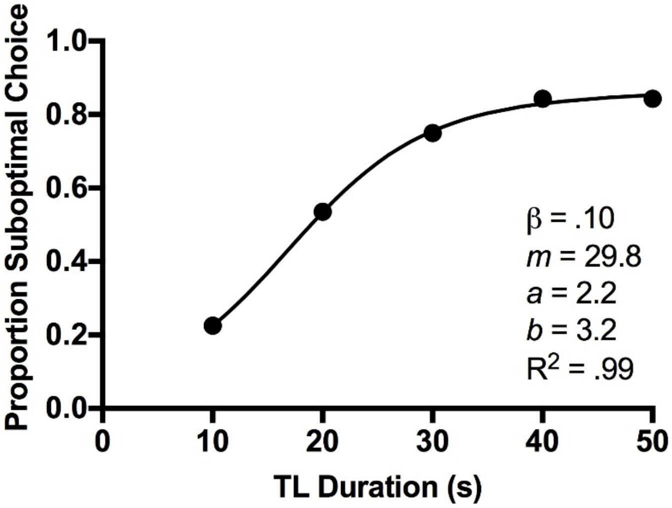

Figure 4. The filled circles depict mean suboptimal choice while the line depicts the fit of the temporal information-theoretic model to mean suboptimal choice.

30 s. Suboptimal choice in the 20 s TL duration condition was not statistically different from indifference, $t(9) = .322$, $p = .754$, $d = .09$.

Figure 4 also depicts the fit of the temporal information-theoretic model to mean suboptimal choice. The temporal information-theoretic model was fit to mean suboptimal choice by minimizing the sum-of-squares deviation using Microsoft Solver. Note that although the figure depicts suboptimal choice as a function of TL duration, the model was fit using D_f/D_s given that the delay to food relative to the signals, and not just TL duration, should govern the weighting mechanism (see Equation 4). The average delay to signals at the choice point is given by: [IL s / pH_{com}], where pH_{com} refers to the probability of receiving any temporally informative TL stimulus (from either alternative). The average delay to food at the choice point is given by: [(IL s + TL s) / pSr], where pSr refers to the average probability of food delivery. The value of D_f/D_s increases with TL duration and assumes the following values for each TL duration (in ascending order): $D_f/D_s = 19$; $D_f/D_s = 36$; $D_f/D_s = 53$; $D_f/D_s = 70$; $D_f/D_s = 87$. We used programmed TL duration along with a 1 s IL duration to obtain these values (consistent with the model fits performed in Cunningham & Shahan, 2018).

It is important to note that the purpose of the model fit was not to assess the adequacy of the temporal information-theoretic model to account for the data. Given the number of free parameters in the model relative to the number of data points, it is not surprising that the model does a good job describing the data. The purpose of the model fit was to obtain parameter estimates in rats that can be compared to obtained parameter estimates in pigeons. In doing so, we hope to provide tentative information about how rats and pigeons might differ in suboptimal choice in terms of the temporal information-theoretic model (e.g., do rats and pigeons differ in sensitivity to relative temporal information? Do they differ in the value of D_f/D_s at which $w = 0.5$?). Although there are no studies equivalent to the present experiment conducted with pigeons, we can draw tentative conclusions by comparing obtained parameter values from the present experiment to the obtained parameter values from Cunningham & Shahan (2018), which were obtained by fitting the temporal information-theoretic model to a wide range of existing suboptimal choice data from pigeons. The obtained parameter values found in Cunningham & Shahan's (2018) model fit to pigeon data suggests the following. First, pigeons appear to have a relatively strong bias for using temporally informative signals to make decisions, suggesting that short delays to food relative to the signals are sufficient to increase w and thereby encourage suboptimal choice ($m = 1.8$). Second, the weighting mechanism in pigeons appears to be hypersensitive to D_f/D_s ($\beta = 1.4$). Third, pigeons appear to be hypersensitive to the relative temporal information conveyed by TL stimuli ($a = 4.4$). Finally, pigeons appear to be only slightly hypersensitive to relative reinforcement rate ($b = 1.4$).

Perhaps the most striking result from the model fit is the relatively high value of m (i.e., 29.8) in rats, indicating that temporally informative signals have to be almost 30 times closer in time than food itself before $w = 0.5$. Further, the sensitivity of w to D_f/D_s, as measured by β and is apparent in the steepness of the fitted curve, appears to be relatively low. The more drastic changes in suboptimal choice as a function of D_f/D_s for individual subjects (see Figure 3) suggests that the more gradual change in the group mean likely resulted from individual differences in value of D_f/D_s (or TL duration) required to induce suboptimal choice. Thus, the obtained value of β for the group mean might be partially obscured by individual differences in *m*, resulting in a slightly underestimated sensitivity of *w* to D_f/D_s (Appendix A presents obtained parameter values from model fits to individual-subject data). Rats, much like pigeons, appear to be hypersensitive to relative temporal information, as indicated by the obtained value of *a* being greater than 1 (i.e., perfect matching). However, rats appear to be slightly less sensitive to relative temporal information than pigeons, as indicated by the value of *a* being twice as large in pigeons than in rats. Finally, rats appear to be more sensitive to relative reinforcement rate than pigeons, as indicated by the value of *b* that is almost three times as large in rats than pigeons.

Discussion

As with previous research, rats in the present experiment did not engage in suboptimal choice with a 10 s TL duration. However, once TL duration was at least 30 s, rats shifted preference from the optimal alternative to the suboptimal alternative. This result suggests that previous failures to find suboptimal choice in rats might have resulted from the fact that TL duration was not long enough. Thus, results from the present experiment suggest that rats readily engage in suboptimal choice as long as the delay to food (i.e., TL duration) is sufficiently long.

Previous failures to find suboptimal choice in rats have given rise to numerous hypotheses about differences in decision-making processes between rats and pigeons. The most often-cited possibility is that rats, unlike pigeons, are sensitive to the conditioned-inhibitory properties of the stimulus never followed by food (i.e., the S-) for the suboptimal alternative (Daniels & Sanabria, 2018; Trujano & Orduña, 2015; Trujano, López, Rojas-Leguizamón, Orduña, 2016). In other words, rats evaluate the suboptimal alternative using the TL stimulus that predicts food (S+) *and* the TL stimulus that is never followed by food (S-), whereas pigeons evaluate the suboptimal alternative using only the food-predictive TL stimulus (Stagner, Laude, & Zentall, 2011). As a result, the value of the suboptimal alternative for rats is thought to be reduced because of the aversive, conditioned-inhibitory properties of the S-, and rats therefore prefer the optimal alternative (see Daniel & Sanabria, 2018 for an associative model of suboptimal choice that addresses the role of sensitivity to conditioned inhibition in suboptimal choice). This possibility would suggest a fundamental difference in the kinds of information pigeons and rats use when making decisions in the suboptimal choice procedure. However, results from the present experiment are difficult to understand in terms of sensitivity to conditioned inhibition. If a 10 s S- is sufficient to discourage suboptimal choice due to its aversive properties, then a 50 s S- should be even more aversive because it signals a longer wait-time in which food is not forthcoming. As a result, one might expect that suboptimal choice should be *less* likely with longer TL durations, whereas the present experiment found that suboptimal choice was more likely. Thus, results from the present experiment suggest that differences in sensitivity to the conditioned-inhibitory properties of the S- might not fully explain differences in suboptimal choice between rats and pigeons.

Another possible reason offered for between-species in suboptimal choice is related to between-species differences in incentive salience attributed to TL stimuli (e.g., Chow et al., 2017; Zentall, Smith, & Beckmann, in press). Incentive salience refers to the “attractive, magnetic” pull of reward-predictive stimuli on behavior and is typically measured by sign-tracking; the degree to which animals’ approach and contact reward-predictive stimuli (Boakes, 1977; Robinson & Berridge, 1993). Stimuli that elicit sign-tracking are typically said to have incentive salience and as a result can encourage highly maladaptive behavior (Flagel, Akil, & Robinson, 2009). Whereas pigeons sign-track localized, food-predictive lights (which are used for TL stimuli in the suboptimal choice procedure for pigeons), rats tend to sign-track small, manipulable objects that predict food (e.g., lever-insertions, Boakes, 1977). If attribution of incentive salience to TL stimuli is required to generate suboptimal choice, then rats should only engage in suboptimal choice when lever-insertions (which do acquire incentive salience) are used as TL stimuli. Chow et al., (2017) found that rats' preference for an alternative offering TL stimuli that differentially signaled choice outcomes over an alternative without differential TL stimuli was more resistant to decreases in the probability of food for the alternative providing differential TL stimuli when those stimuli were levers (which acquire incentive salience) compared to lights. Thus, the attribution of incentive salience to TL stimuli might be both necessary and sufficient for suboptimal choice. Previous failures to find suboptimal choice in rats might simply have resulted from the fact that TL stimuli used in previous experiments did not provide the right stimulus-support for rats to attribute incentive salience to the TL stimuli (i.e., the LED lights used in Trujano & Orduña, 2015). However, numerous experiments since Chow et al., (2017) have failed to find acquisition of suboptimal choice in rats when lever-insertions were used as TL stimuli (e.g., Alba et al., 2018; Martinez et al., 2017). Further, López, Alba, & Orduña (2017) explored the possibility that rats that are more likely to assign incentive salience to food-predictive stimuli, as measured by sign-tracking, are more likely to engage in suboptimal choice. Indeed, there is a growing literature showing that individual differences in the tendency to sign-track food-predictive stimuli correlates with a variety of maladaptive behaviors in rats (see Flagel et al., 2009 for review). However, López et al., did not find suboptimal choice in any rats, regardless of the degree to which they sign-tracked food-predictive stimuli (i.e., levers). Thus, the current body of evidence suggests that incentive salience attribution to TL stimuli is not sufficient to encourage suboptimal choice in rats.

Results from the present experiment might also suggest that incentive salience is not necessary for suboptimal choice, given that rats in the present experiment readily made suboptimal choices despite the use of lights and tones (which do not elicit sign-tracking responses) as TL stimuli. Thus, the current body of evidence suggests that incentive salience is neither necessary nor sufficient for suboptimal choice in rats. Nevertheless, it is possible that TL stimulus modality (and its incentive salience) might play a role in suboptimal choice, though its role is currently unclear (see Zentall, et al., in press for a framework to understand the possible role of TL-stimulus modality in suboptimal choice). Indeed, the potential role of stimulus modality might explain the discrepant results between the present experiment and Trujano & Orduña (2015), who, unlike the present experiment, did not find suboptimal choice with a 30 s TL duration. Perhaps the reason for this difference is that the tone + light stimuli used in the present experiment was more salient than the small LED bulbs used in Trujano & Orduña (2015) and might therefore be more prone to serve as conditioned reinforcers when established as temporally informative stimuli. Thus, stimulus modality (and incentive salience) could interact with Pavlovian factors (e.g., the temporal information conveyed by stimuli) to govern the degree to which stimuli serve as conditioned reinforcers. This possibility is only speculative, and more research is required to further clarify the potential role of stimulus modality (and incentive salience) in the ability of stimuli to function as conditioned reinforcers and thereby encourage maladaptive decision-making.

Although results from the present experiment are difficult to reconcile with previous hypotheses about suboptimal choice in rats (e.g., conditioned inhibition and incentive salience), they appear consistent with the Signals for Good News (SiGN) Hypothesis (McDevitt et al., 2016) and our temporal information-theoretic model (Cunningham & Shahan, 2018). The SiGN Hypothesis suggests that choice is governed by both the conditioned-reinforcing efficacy of TL stimuli and the primary-reinforcing efficacy of delayed food. Importantly, food exerts less control over choice as its delay increases. As a result, as the delay to food increases choice becomes less influenced by food and more influenced by the conditioned-reinforcing efficacy of TL stimuli. Thus, the SiGN Hypothesis predicts more suboptimal choice with longer TL durations and is therefore consistent with results from the present experiment. However, one limitation of the SiGN Hypothesis is that it is currently not formalized and does not permit quantitative predictions.

On the other hand, the temporal information-theoretic model provides a formalized quantitative account specifying which aspects of the suboptimal choice procedure influence choice (e.g., IL and TL durations, the probability of food delivery, the predictive relation between TL stimuli and food) along with free parameters that can be used to suggest potential differences and similarities in suboptimal choice between rats and pigeons. According to the temporal information-theoretic model, as TL duration increases, the delay to food at the choice point (D_f) increases. As a result, the ratio D_f/D_s

increases and animals should give more weight to relative temporal information rather than relative reinforcement rate to make decisions. As a result, preference for the suboptimal alternative should emerge with increases in TL duration. Thus, within the temporal information-theoretic framework, differences in suboptimal choice between rats and pigeons might not reflect fundamental differences in the decision-making processes that govern suboptimal choice, but instead might reflect differences in the value of D_f/D_s required to generate suboptimal choice.

These between-species differences would appear primarily in the free parameters that govern the impact of D_f/D_s on the weighting function (i.e., m and β). By comparing obtained parameter values from the weighting function in rats (from the present experiment) and parameter values that account for a majority of suboptimal choice data in pigeons (see Cunningham & Shahan, 2018), we can draw tentative conclusions about potential differences in suboptimal choice between rats and pigeons in terms of the temporal information-theoretic model. First, rats appear to have a much stronger bias *against* using temporally informative signals to make decisions than pigeons (i.e., m is much higher in rats than pigeons). Second, the weighting mechanism in rats appears to be less sensitive to variations D_f/D_s than pigeons (i.e., β is smaller in rats than pigeons). However, more definitive conclusions about quantitative differences in suboptimal choice between rats and pigeons must await future research directly comparing suboptimal choice between the two species under identical procedural conditions. Our analysis here is meant only as a preliminary comparison based on available evidence.

In sum, the temporal information-theoretic model of suboptimal choice suggests that the bits of temporal information conveyed by TL stimuli and the rate of reinforcement afforded by suboptimal and optimal alternatives compete to control choice. Suboptimal choice arises when relative temporal information contributes more heavily to choice than relative reinforcement rate. In this sense, the temporal information-theoretic model formalizes the notion that suboptimal choice reflects an animal's willingness to sacrifice food in order to receive information about food (Vasconcelos et al., 2015); to prefer "bits" over "bites". Results from the present experiment suggest that rats, like pigeons, are susceptible to make bad decisions when they are provided an opportunity to earn bits of (temporal) information even though doing so is not in their long-term best interest. Thus, the tendency of animals to track and respond for bits of information might reflect a species-general phenomenon that yields important insights into the ways in which animals incorporate food-predictive stimuli (i.e., "conditioned reinforcers") into decision-making processes which can sometimes lead to maladaptive results. Results from the present experiment suggest that the suboptimal choice procedure can indeed be used with rats to study the role of food-predictive stimuli in maladaptive decision-making. Use of the suboptimal choice procedure with rats might also serve as a more useful platform for elucidating the neurobiological mechanisms of how reward-predictive stimuli contribute to clinically-relevant maladaptive decision-making (e.g., gambling disorder, substance abuse).

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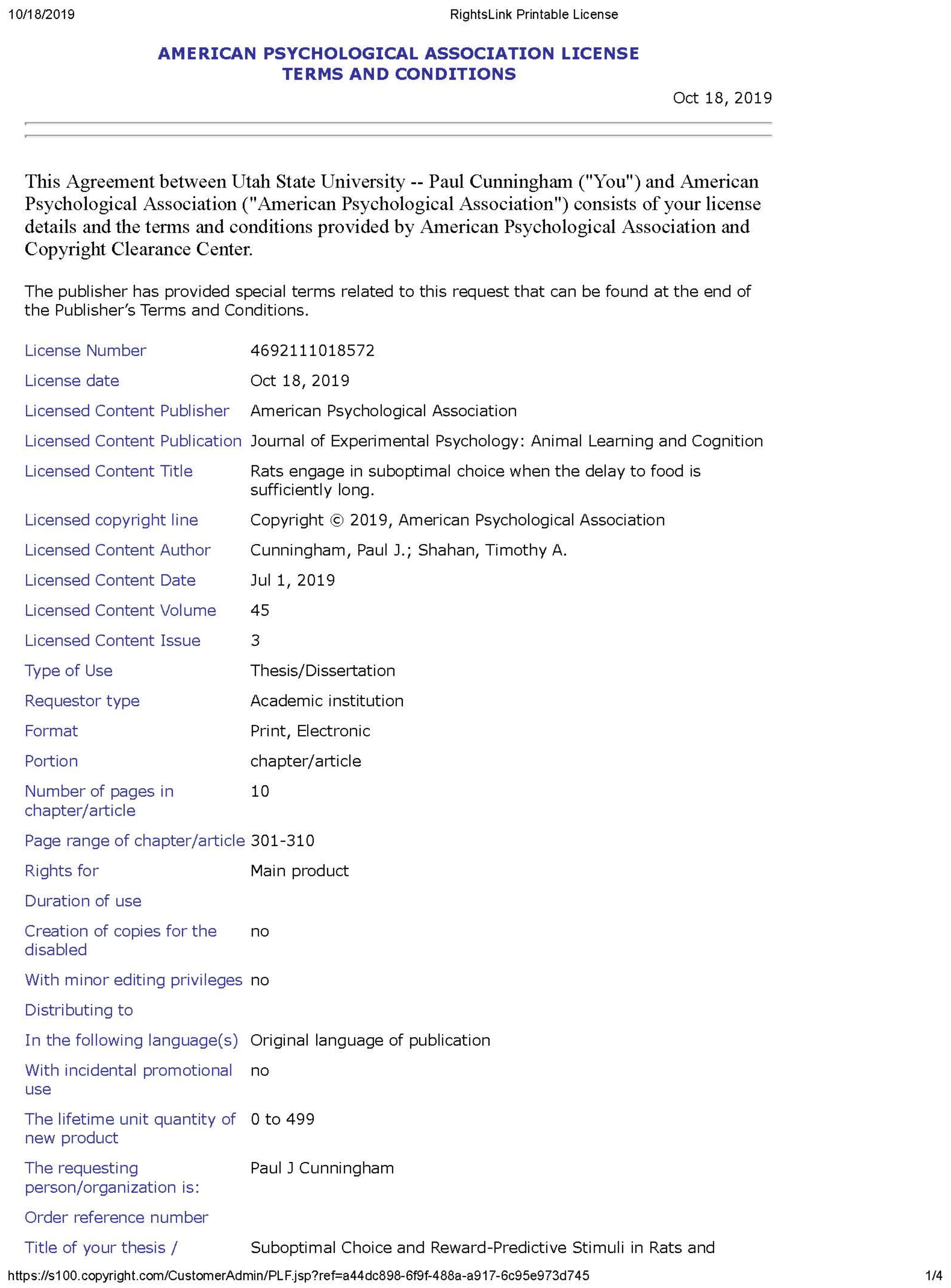
Appendix A

Table 1. Obtained parameter values from the temporal information-theoretic model for individual subjects.

Rat	*a*	*b*	*m*	β	R^2
K21	1.9	1.4	55.4	.23	.99
K22	12.2	2.3	16.2	.39	.99
K23	4.1	8.7	30.3	.95	.99
K24	4.2	2.3	34.6	.38	.99
K25	2.8	16.9	42.5	.13	.99
K26	5.7	1.1	17.9	.47	.99
K27	2.3	18.1	37.5	.22	.96
K28	3.5	1.2	50.9	.30	.99
K29	1.5	11.2	26.9	.19	.96
K30	1.0	1.7	91.7	.51	.06

Appendix B



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CHAPTER 4

Delays to Temporally Informative Signals Do Not Affect Suboptimal Choice in Rats

Abstract

Suboptimal choice represents a form of maladaptive decision-making in which pigeons repeatedly choose an option providing food-predictive stimuli even though they earn less food for doing so. The temporal information-theoretic model suggests that suboptimal choice depends on competition between the bits of temporal information conveyed by food-predictive stimuli (which encourages suboptimal choice) and the rate of food delivery (which encourages optimal choice). The model assumes that competition between these two sources of control is based on the ratio of the delay to food (D_f) and the delay to food-predictive stimuli (D_s) at the choice point (i.e., D_f/D_s). Research with both rats and pigeons suggests that temporal information outcompetes the rate of food delivery, thereby generating suboptimal choice, when the delay to food (D_f) is sufficiently long. Very limited data with pigeons, and none with rats, suggests that the rate of food delivery outcomes temporal information, thereby generating optimal choice, when the delay to food-predictive stimuli (D_s) is sufficiently long. The present experiment sought to clarify whether longer delays to food-predictive stimuli decreased suboptimal choice in rats. We found that while longer delays to food (Df) increased suboptimal choice in rats, longer delays to food-predictive stimuli (D_s) did not decrease suboptimal choice. These results suggest a potential difference between rats and pigeons in the manner in which food-predictive stimuli and food itself compete to control choice.

In terms of the temporal information-theoretic model, competition between temporal information and the rate of food delivery in rats is influenced only by the delay to food at the choice point.

Key words: Suboptimal Choice, Rats, Temporal Information, Conditioned Reinforcement, Information Theory

Introduction

The processes that govern decision-making in animals are often considered within a normative context, from ultimate explanations based on Optimal foraging theory (Stephens & Krebs, 1986) to proximate explanations based on algorithms that learn and select actions that lead to the most food (Rangel, Carmerer, & Montague, 2008). However, there are numerous examples illustrating maladaptive susceptibilities in animal decision-making processes. These examples of maladaptive decision-making are difficult to reconcile with normative perspectives. As such, the study of maladaptive decision-making can provide novel insights into the kinds of information animals use to make decisions and the ways in which various sources of information interact to govern choice (e.g., Fantino, 2012; Igaki, Romanowhich, & Sakagami, 2019; Vasconcelos, Machado, Pandeirada, 2018; Zentall, 2014). Suboptimal choice is one such example that highlights an important role for food-predictive stimuli in maladaptive decision-making.

Figure 1 depicts the decision-making procedure commonly used to study suboptimal choice in pigeons. In this procedure, pigeons are given a choice between two response options that produce delayed, probabilistic food. Responses to one of the options during the initial-link (IL) choice phase results in a transition to the terminal-link (TL), which is defined by a delay that ends probabilistically with food. The duration of the TL (i.e., the delay between a choice response and trial outcome) is the same for each alternative, but the probability of food differs between alternatives. One alternative, referred to as the suboptimal alternative, offers a lower probability of food (e.g., $pSr = 0.2$) than the other, optimal, alternative (e.g., $pSr = 0.5$). Importantly, only the suboptimal alternative provides TL stimuli that differentially signal food delivery, with one TL stimulus always followed by food (i.e., the S+) and the other TL stimulus never followed by food (i.e., the S-). Although the suboptimal alternative offers less food than the optimal alternative, pigeons show a strong preference for the suboptimal alternative (for reviews, see Cunningham & Shahan, 2018; McDevitt et al., 2016; Zentall, 2016). For this reason, preference for the suboptimal alternative is referred to as suboptimal choice.

Research suggests that suboptimal choice arises because pigeons make their decisions based on the predictive relation between TL and food rather than the overall probability (or rate) of food delivery. Suboptimal choice therefore arises because pigeons are more attracted to the food-predictive TL stimulus for the suboptimal alternative (i.e., the S+) than TL stimuli for the optimal alternative that are only sometimes followed by food. In this way, suboptimal choice reflects an interesting example of maladaptive decision-making in which pigeons sacrifice food to receive information about food. Thus, the study of suboptimal choice has the potential to reveal important insights into the

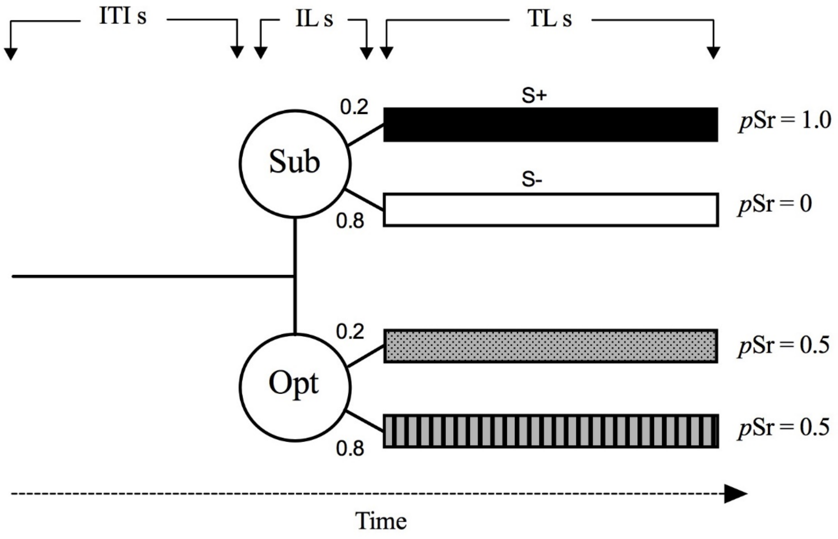

Figure 1. Depiction of the suboptimal choice procedure in which the suboptimal alternative provides TL stimuli that differentially signal food while the optimal alternative does not.

manner in which informative, food-predictive stimuli influence decision-making in a manner that can sometimes result in maladaptive outcomes.

In addition, some have argued that the decision-making processes that govern suboptimal choice in pigeons might contribute to problematic gambling in humans (Molet et al., 2014; Zentall & Stagner, 2011; Zentall, 2014). It is argued that the stimulus-complex accompanying a winning pull on a slot machine (i.e., the reward-predictive stimuli) encourages individuals to continue gambling even though they lose money in the long run for doing so, much like pigeons continue choosing an alternative offering food-predictive stimuli even though they lose food in the long run for doing so. Thus, the study of suboptimal choice in pigeons has the potential to reveal important insights into 1) the manner in which reward-predictive stimuli influence choice, and 2) how reward-predictive stimuli contribute to maladaptive decisions that define problematic gambling in humans.

Although suboptimal choice is well documented in pigeons, its species-generality has been questioned given numerous failed attempts to find suboptimal choice in rats under conditions that reliably generate suboptimal choice in pigeons (Alba et al., 2018; Lopez, Alba, & Orduña, 2018; Martinez et al., 2017; Ojeda, Murphy, & Kacelnik, 2018; Orduña & Alba, 2019; Trujano & Orduña, 2016; Trujano, López, Rojas-Leguizamón, & Orduña, 2016). In other words, unlike pigeons, rats do not appear to be willing to sacrifice food for food-predictive stimuli. If suboptimal choice is a phenomenon specific to pigeons, its utility as means of understanding the role of reward-predictive stimuli in maladaptive decision making, along with its potential clinical implications, is limited. Thus, a major goal of suboptimal choice research is to explore differences and similarities in the decision-making processes involved in suboptimal choice between rats and pigeons.

Cunningham & Shahan (2018) proposed a quantitative model that accurately describes the variables influencing suboptimal choice in pigeons. This model can be used to inform experiments on suboptimal choice in rats and provide a framework for understanding potential species-differences in suboptimal choice. Cunningham & Shahan's temporal information-theoretic model consists of three parts that collectively determine preference between suboptimal and optimal alternatives in pigeons.

The first part of the model states that TL stimuli influence choice based on the temporal information they convey (i.e., the information TL stimuli convey about *when* to expect food). The notion that TL stimuli influence choice based on their temporal information derives from the well-established role of temporal information in Pavlovian conditioning (see Balsam et al., 2010), along with the notion that Pavlovian conditioning governs the ability of food-predictive stimuli to influence instrumental behavior (Mackintosh, 1974; Shahan, 2010; 2017; Shahan & Cunningham, 2015; Williams, 1994). Temporal information is quantified by applying Shannon's information-theoretic measure of uncertainty, entropy, to the probability distribution of 1) intervals between food deliveries independent of anything else in the session (i.e., the food-food interval), and 2) intervals between stimulus onset and food delivery (i.e., the stimulus-food interval). Probability distributions for the food-food intervals and stimulus-food intervals are assumed to be exponential, though calculations of temporal information can readily be applied to distributions other than exponential (see Gallistel & Balsam, 2009; Balsam et al., 2010).

The average (basal) uncertainty about when to expect food in an experimental session depends on the average interval between food deliveries independent of anything else in the session (i.e., the food-food interval). The average uncertainty about when to expect food in the presence of the stimulus depends on the average interval between stimulus onset and food delivery (i.e., the stimulus-food interval). Temporal information conveyed by the stimulus is then quantified by taking the difference between the average uncertainty about when to expect food in the experimental session and the average uncertainty about when to expect food in the presence of the stimulus:

$$H = (log_2 C + k) - (log_2 t + k) = log_2(C/t) \qquad (1).$$

H represents the bits of temporal information conveyed by a food-correlated stimulus, C represents the average food-food interval (i.e., overall average uncertainty), t represents the average stimulus-food interval (i.e., uncertainty in the presence of the stimulus), and k is a constant that depends on the resolution with which animals represent time (for more detailed discussion, see Balsam et al., 2010; Cunningham & Shahan, 2018; Shahan & Cunningham, 2015). Stimuli that signal a greater reduction in the delay to food (i.e., smaller values of t) relative to the average delay to food in the experimental session (C) convey more temporal information.

According to the temporal information-theoretic model, pigeons should prefer the alternative offering the more temporally informative TL stimulus, according to the equation:

$$\frac{H_{Sub}^{a}}{H_{Sub}^{a} + H_{opt}^{a}} \qquad (2),$$

where a reflects the sensitivity of choice to relative temporal information. When the suboptimal, but not optimal, alternative provides TL stimuli that differentially signal food (see Figure 1), the S+ for the suboptimal alternative conveys more temporal information than the TL stimulus only sometimes followed by food for the optimal alternative (see Cunningham & Shahan, 2018 for detailed discussion of why this is so). Thus, framing the influence of TL stimuli on choice in terms of temporal information captures the reason why the suboptimal S+ attracts more choice responses than the optimal TL stimuli in a manner consistent with quantitative formulations of Pavlovian conditioning (Balsam et al., 2010) and conditioned reinforcement (Shahan & Cunningham, 2015).

The second part of the temporal information-theoretic model assumes that the rate of food delivery also influences choice according to the matching law (Herrnstein, 1961; Baum, 1974):

$$\frac{R_{Sub}^{b}}{R_{Sub}^{b} + R_{opt}^{b}} \qquad (3),$$

where R denotes the rate of food delivery for suboptimal and optimal alternatives and *b* reflects the sensitivity of choice to the relative rate of food delivery. According to Equation 3, pigeons should prefer the alternative providing the higher rate of food delivery, which is the optimal alternative in the suboptimal choice procedure. Thus, according to the temporal information-theoretic approach, the relative temporal information conveyed by TL stimuli and the relative rate of food delivery compete to control choice:

$$pSub = w\frac{H_{sub}^{a}}{H_{sub}^{a} + H_{opt}^{a}} + (1 - w)\frac{R_{sub}^{b}}{R_{sub}^{b} + R_{opt}^{b}} \qquad (4),$$

where *w* governs the weight given to relative temporal information as a determinant of choice and its complement, 1 – *w*, governs the weight given to the relative rate of food delivery as a determinant of choice. In the suboptimal choice procedure, relative temporal information (Equation 2) pulls choice to the suboptimal alternative while the relative rate of food delivery (Equation 3) pulls choice to the optimal alternative. Thus, preference for the suboptimal alternative can happen only when *w* is close to 1 and relative temporal information has a stronger grip on choice than the relative rate of food delivery.

The third part of the temporal information-theoretic model defines the weighting mechanism (i.e., *w*) and is based on studies assessing the influence of IL and TL duration on suboptimal choice in pigeons. Numerous experiments with pigeons found that suboptimal choice increases with longer TL durations, suggesting that longer delays to food increases the likelihood of suboptimal choice (Dunn & Spetch, 1990; McDevitt et al., 2018; Spetch et al., 1990; Spetch et al., 1994). Based on these data, the temporal information-theoretic model assumes that the delay to food contributes to competition between relative temporal information and the relative rate of food delivery to determine choice.

While the evidence is clear that suboptimal choice increases with longer TL durations, it is currently less clear whether IL duration influences suboptimal choice. Limited evidence suggests that longer IL durations decrease suboptimal choice (e.g., Experiment 3 from Dunn & Spetch, 1990). Further, there is some evidence suggesting that long TL durations do not increase suboptimal choice when IL duration is sufficiently long (Experiment 2 from Dunn & Spetch, 1990). However, longer IL durations do not always decrease suboptimal choice (e.g., Experiment 1 from Dunn & Spetch, 1990) and the influence of IL duration on suboptimal choice can be inconsistent across pigeons (e.g., Zentall, Andrews, & Case, 2017). Given the uncertainty surrounding such effects, some theories of suboptimal choice do not include a role for IL duration (e.g., Daniels &

Sanabria, 2018; Zentall, 2016). Nevertheless, based on these limited data, the temporal information-theoretic model assumes that longer delays to temporally informative TL stimuli (via longer IL durations) decreases the likelihood of suboptimal choice in pigeons by influencing competition between relative temporal information and the relative rate of food delivery (i.e., *w*).

The temporal information-theoretic model accounts for the influence of IL and TL duration on suboptimal choice with the assumption that the weighting mechanism is governed by the average delay to food at the choice point relative to the average delay to the temporally informative TL stimuli at the choice point (with the choice point is defined by the moment at which the choice is presented to the animal):

$$w = \frac{1}{1 + e^{-\beta\left(\frac{D_f}{D_s} - m\right)}} \qquad (5).$$

D_f denotes the average delay to food at the choice point, D_s denotes the average delay to temporally informative stimuli at the choice point, beta represents the sensitivity of *w* to variations in D_f/D_s and *m* represents the value of D_f/D_s at which $w = 0.5$.

According to Equation 5, as TL duration increases the average delay to food at the choice point (D_f) increases while the delay to TL stimuli (D_s) remains unchanged. Thus, longer TL durations result in larger values of D_f/D_s and, as a result, relative temporal information holds more weight as a determinant of choice. Under these conditions, suboptimal choice emerges. Alternatively, as IL duration increases the delay to temporally informative TL stimuli at the choice point (D_s) increases. As a result, D_f/D_s decreases and the relative rate of food delivery holds more weight as a determinant of choice. Under these conditions, optimal choice emerges. Thus, the novel weighting mechanism defined by Equation 5 describes the manner in which relative temporal information and the relative rate of food delivery compete to control choice. Inserting Equation 5 into Equation 4 suggests that suboptimal choice emerges when 1) TL stimuli for the suboptimal alternative convey more temporal information than the optimal alternative, and 2) temporally informative TL stimuli are much closer in time than food itself at the choice point.

Previous research suggests that a 10 s TL duration is sufficiently long to generate suboptimal choice in pigeons. For this reason, it is perhaps not surprising that initial research with rats, which failed to find suboptimal choice, also used a 10 s TL duration. However, there is reason to believe that rats require a longer delay to food than pigeons before engaging in suboptimal choice. Evidence from the inter-temporal choice literature suggest that rats tolerate longer delays to food than pigeons before preferring a maladaptive smaller, immediate food in lieu of an adaptive larger, delayed food (Green et al., 2004; Mazur, 2000; Mazur & Biondi, 2009; Tobin & Logue, 1994). Thus, it is possible that rats will readily engage in suboptimal choice once the delay to food at the choice point is sufficiently long. The temporal information-theoretic model captures this through the influence of TL duration on D_f, and therefore *w*.

Cunningham & Shahan (2019) explored the possibility that rats engage in suboptimal choice once the delay to food is sufficiently long. Rats were given a choice between a suboptimal alternative providing food 20% of the time, with differential TL stimuli, and an optimal alternative providing food 50% of the time without differential TL stimuli. A single choice response in the IL (i.e., the shortest possible programmed delay to TL stimuli) resulted in a transition to the TL whose duration varied from 10 s to 50 s across conditions. Cunningham & Shahan (2019) found that 1) rats did not engage in suboptimal choice when TL duration was 10 s, and 2) rats engaged in suboptimal choice once TL duration was at least 30 s. These results suggest that rats readily engage in suboptimal choice when the delay to food at the choice point is sufficiently long. In terms of the temporal information-theoretic model, increases in the delay to food at the choice point increases suboptimal choice by increasing D_f/D_s, resulting in decisions based on relative temporal information rather than the relative rate of food delivery.

While the results from Cunningham & Shahan (2019) demonstrated that rats indeed engage in suboptimal choice provided a sufficiently long delay to food, it is still unclear if the delay to food increases suboptimal choice through its impact on D_f/D_s, as Equation 5 suggests. The limited evidence available suggests that suboptimal choice in pigeons decreases with longer delays to the TL stimuli at the choice point (i.e., D_s) via longer IL durations. For this reason, the weighting mechanism in the temporal information-theoretic model is not governed solely by D_f, but is instead governed by an interaction between D_f and D_s. The ratio D_f/D_s appears to be the best way to capture the interaction between D_f and D_s in a manner consistent with available data in pigeons. There are currently no published studies examining the influence of IL duration, and therefore delays to temporally informative TL stimuli, on suboptimal choice in rats. Thus, the purpose of the present experiment was to assess whether the weighting mechanism in rats is governed by D_f/D_s or just D_f. Can the increase in suboptimal choice with increases in D_f be offset by increases in D_s, as it appears to in pigeons? In addition, is the degree of suboptimal choice invariant with D_f/D_s in rats as it appears to be in pigeons?

In the present experiment, rats were given a choice between a suboptimal alternative providing food 20% of the time with differential TL stimuli and an optimal alternative providing food 50% of the time without differential TL stimuli (see Figure 1). IL and TL durations varied across four conditions. Two conditions consisted of a FR 1 IL schedule with a 10 s and 50 s TL duration, replicating the shortest and longest TL-duration conditions from Cunningham & Shahan (2019). A third, novel condition assessed suboptimal choice with a fixed-interval (FI) 5 s IL schedule and a 50 s TL duration. This third condition arranged a value of D_f similar to the 50 s TL replication condition, but a value of D_f/D_s identical to the 10 s TL replication condition (via an increase in IL duration and therefore D_s). If the ratio D_f/D_s governs the weighting mechanism in rats, then preference for the optimal alternative is expected in this third, novel condition and to the same extent as in the 10 s TL replication condition. However, if only the delay to food at the choice point (D_f) is important, then rats should prefer the suboptimal alternative in the third, novel condition (i.e., increasing D_s should have no effect on suboptimal choice). Finally, a fourth condition assessed suboptimal choice with a FI 10 s IL schedule in conjunction with a 50 s TL duration to see if further decreases in D_f/D_s resulted in further decreases in suboptimal choice, as the temporal information-theoretic model predicts.

Methods

Subjects. Sixteen male Long-Evans rats (Charles River, Portage, MI), approximately 280 days old at the start of the experiment, served as subjects. Rats were individually housed in a temperature-controlled colony room with a 12:12 light/dark cycle. Rats were maintained at 80% of their free-feeding weight and had free access to water in their home cages. All rats had previous experience with lever-pressing for food under variable-interval schedules reinforcement and extinction. Animal housing and care, and all procedures used, were conducted in accordance with Utah State University's Institutional Animal Care and Use Committee.

Apparatus. Ten identical modular operant chambers (Med Associates, St. Albans, VT), each housed in a sound-attenuating cubicle, were used. Each chamber was constructed of clear Plexiglas with aluminum work panels on the front and back walls. Near the bottom on the center panel of the front wall was a feeder aperture into which 45 mg grain-based food pellets (Bio Serv, Flemington, NJ) were delivered. Pellet deliveries were accompanied by 3-sec feeder illumination with a 28 vdc feeder light. Two retractable levers with stimulus lights above each were located equidistant from the feeder aperture to the left and right of the center panel. A 28 vdc houselight was located at the top of the center panel on the front wall of the chamber. Finally, a tone-generator was located in the upper-left corner of the front panel.

Procedure. Prior to the suboptimal choice procedure, all rats received 5 sessions of lever-press training in which either the right or left lever, was inserted into the chamber on a pseudo-random basis, with the constraint that neither lever could be presented more than twice in a row. A single lever press immediately delivered food, after which a 10 s inter-trial interval (ITI) ensued. Following the 10 s ITI, the next trial began. Each lever was presented 24 times per session. The purpose of this training was to ensure that rats pressed each lever with approximately the same latency before the experiment proper began.

The suboptimal choice procedure consisted of a choice between a suboptimal alternative delivering food 20% of the time and an optimal alternative delivering food 50% of the time. The probability of food was determined by querying a probability gate each time the lever was pressed. Suboptimal and optimal alternatives were defined by left and right levers (counterbalanced across subjects). Choice outcomes were signaled by TL stimuli for the suboptimal alternative but not for the optimal alternative. The food-predictive TL stimulus for the suboptimal alternative and the TL stimulus for the optimal alternative consisted of a constant or flashing (1 flash/sec) stimulus-light + tone combination (counterbalanced across subjects). The stimulus light was located above the lever defining a given alternative.

Each session consisted of 48 forced-exposure trials and 24 free-choice trials. Trial-types were randomly presented in blocks of three such that every three trials consisted of two forced-exposure trials (one for each alternative) and one free-choice trial. Each trial started with a centering response in which the feeder was illuminated and the rat poked his head into the feeder. Once this centering response was made, the houselight turned on and the choice lever (or levers, depending on trial type) was inserted into the chamber. On forced-exposure trials, either the suboptimal or optimal lever was extended into the chamber. During conditions with a FR 1 IL schedule, a single response to the lever resulted in a transition to the TL. During conditions with a FI 5 s or FI 10 s IL schedule, the first lever press following 5 s or 10 s after lever insertion resulted in transition to the TL. The transition to the TL was signaled by lever retraction, the houselight turning off, and the TL stimulus turning on. For the suboptimal alternative, the stimulus-light + tone compound was presented if food was forthcoming (i.e., the S+) whereas all stimuli turned off if food was not forthcoming (i.e., the S-). For the optimal alternative, the stimulus-light + tone compound was always presented during the TL. The TL ended with either a single food pellet or a 3 s blackout. Free-choice trials were the same as forced-exposure trials with the exception that both suboptimal and optimal levers were extended into the chamber. For free-choice trials in conditions with a FI IL schedule, the first press to one of the choice levers retracted the other lever (e.g., if the rat made a lever press to the suboptimal alternative before the FI schedule had elapsed, the optimal lever was retracted). Each trial was separated by a 10 s ITI.

Rats experienced each of four conditions with various combinations of IL and TL durations. In one condition, termed short-short, the IL consisted of a FR 1 schedule with a 10 s TL duration. In another condition, termed short-long, the IL consisted of a FR 1 with a 50 s TL duration. In the third condition, termed long-long, a FI 5 s schedule was operative in the IL with a 50 s TL duration. In the fourth condition, termed extra-long-long, a FI 10 s schedule was operative in the IL with a 50 s TL duration. The short-short, short-long, and long-long conditions were presented in a counterbalanced order across rats. The extra-long-long condition was presented last for each rat.

The short-short and short-long conditions are identical to the two most extreme TL-duration conditions from Cunningham & Shahan (2019). The purpose of including the long-long and extra-long-long conditions was to assess 1) whether longer IL durations reduce suboptimal choice in rats, and 2) whether suboptimal choice is governed by the

Table 1. Values of D_f and D_f/D_s across conditions

Condition	IL	TL	D_s	D_f	D_f/D_s	Prediction
Short-Short	FR 1	10 s	≈1.6 s	≈31.4 s	≈18.9	Optimal Choice
Short-Long	FR 1	50 s	≈1.6 s	≈145.7 s	≈87.4	Suboptimal Choice
Long-Long	FI 5 s	50 s	≈8.3 s	≈157.1 s	≈18.9	Optimal Choice
Extra-Long-Long	FI 10 s	50 s	≈16.6 s	≈171.4 s	≈10.3	Optimal Choice

Note. D_s is calculated as [IL s/*p*H], where *p*H refers to the probability of receiving *any* temporally informative signal (i.e., from either alternative) on a given trial. D_f is calculated as [(IL + TL s)/*p*Sr], where *p*Sr refers to the overall probability of receiving food (from either alternative) on a given trial. Thus, delays to both temporally informative signals and food are not calculated independently between alternatives, but are instead a global average. Finally, IL duration with a FR 1 schedule was assumed to be 1 s for these calculations.

ratio D_f/D_s as Equation 5 suggests. Because D_f/D_s is identical between conditions short-short and long-long, the model predicts the same degree of optimal choice under these conditions. In addition, because D_f/D_s is smaller in the extra-long-long condition than the long-long condition, rats should show the strongest preference for the optimal alternative in the extra-long-long condition.

Results

Rate of feeder entries in the presence of the TL stimuli was examined to ensure that rats indeed learned about the relation between TL stimuli and food. Figure 2 shows mean rate of feeder entries in each of the three TL stimuli across all four conditions, averaged from the last 5 days of each condition. A 3 X 4 (TL stimulus X condition) repeated measures analysis of variance (ANOVA) revealed a significant main effect of TL stimulus, $F(2,30) = 71.46$, $p < .001$, a significant main effect of condition, $F(3,45) = 6.73$, $p = .001$, and a significant TL stimulus by condition interaction, $F(6,90) = 3.05$, $p =$

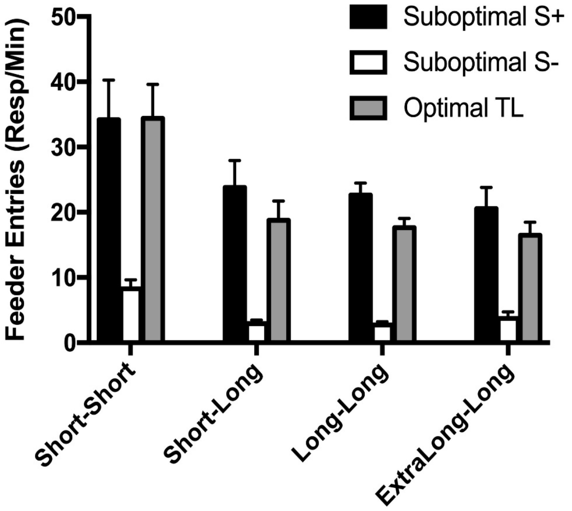

Figure 2. Mean rate of feeder entries in the suboptimal S+ (black bars), the suboptimal S- (white bars), and the optimal TL stimulus (gray bars). Error bars represent standard error of the mean (SEM).

.009. The interaction resulted from a greater difference in feeder entries between the optimal TL stimulus and the suboptimal S- in the short-short condition compared to all other conditions. This was revealed through several follow-up repeated measures ANOVAs revealing a significant interaction between feeder entries in the optimal TL stimulus and the suboptimal S- in the short-short and short-long condition, *F*(1,15) = 4.89, *p* = .04, the short-short and long-long condition, *F*(1,15) = 6.42, *p* = .02, and the short-short and extra-long-long condition, *F*(1,15) = 9.73, *p* = .007. Thus, there was a smaller difference in feeder entries between the optimal TL stimulus and the suboptimal S- when TL duration was long (i.e., 50 s) compared to when it was short (i.e., 10 s). Nevertheless, as is clear from Figure 2, rats showed a higher rate of feeder entries in the presence of the suboptimal S+ and the optimal TL stimulus than in the presence of the suboptimal S-. This was true for each of the four conditions. These results suggest that

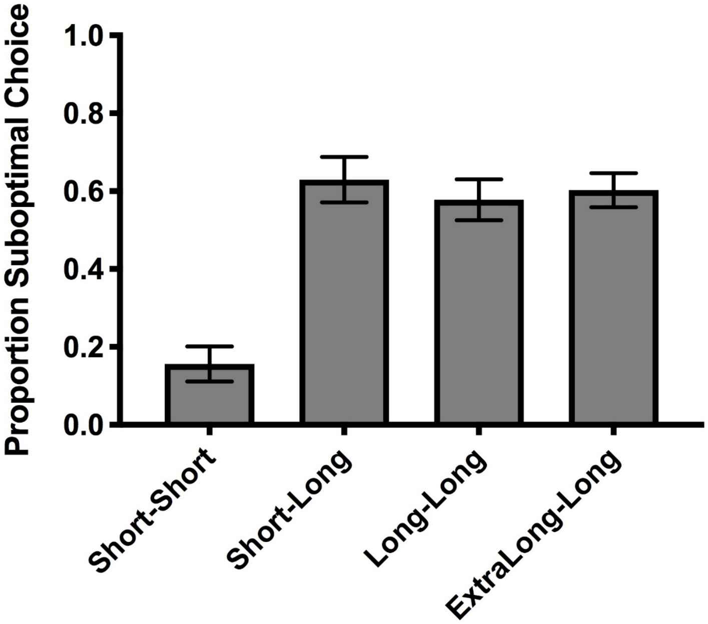

Figure 3. Mean suboptimal choice across conditions. Error bars represent SEM.

rats indeed discriminated between TL stimuli and learned which ones were and were not followed by food.

Figure 3 depicts mean proportion suboptimal choice across conditions, averaged from the last 5 days of each condition. A one-way repeated measures ANOVA revealed a significant effect of condition on suboptimal choice, $F(4,45) = 35.25$, $p < .001$. Follow-up analysis revealed a significant difference in suboptimal choice between the short-short condition and the short-long condition, $F(1,15) = 47.31$, $p < .001$, the long-long condition, $F(1,15) = 102.46$, $p < .001$, and extra-long-long condition, $F(1,15) = 85.50$, $p < .001$. Thus, increasing the delay to food at the choice point enhanced suboptimal choice. However, there were no differences in suboptimal choice between the short-long, long-long, and extra-long-long conditions. Thus, longer IL durations did not reduce suboptimal choice in rats.

Figure 4 shows a comparison of suboptimal choice between the short-short and short-long conditions (left panel), the short-short and long-long conditions (center panel), and the short-short and extra-long-long conditions (right panel) for individual rats.

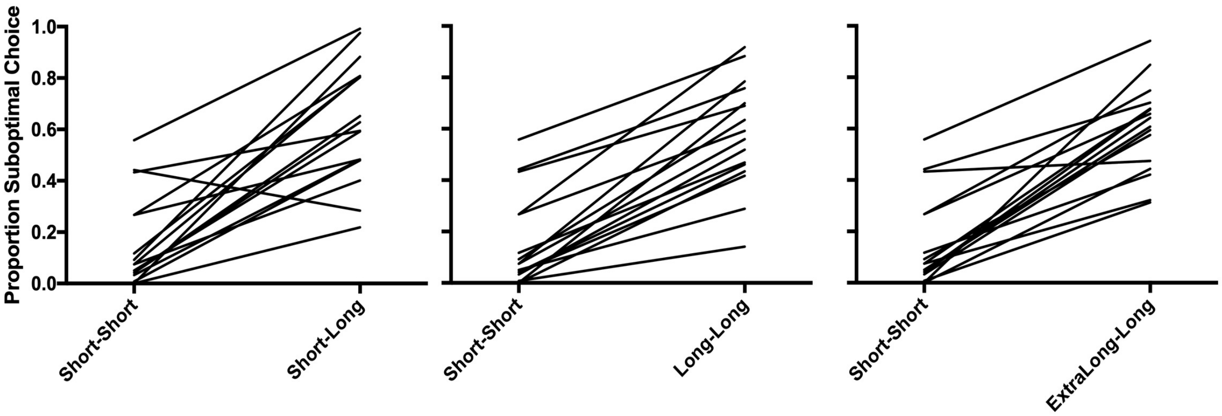

Figure 4. Left Panel: Individual subject comparison of suboptimal choice between the short-short and short-long conditions. Middle Panel: Individual subject comparison of suboptimal choice between the short-short and long-long conditions. Right Panel: Individual subject comparison of suboptimal choice between the short-short and extra-long-long conditions.

Relative to the short-short condition, the model with a weighting mechanism defined by Equation 5 predicts 1) more suboptimal choice in the short-long condition, 2) the same amount of suboptimal choice in the long-long condition, and 3) less suboptimal choice in the extra-long-long condition. Consistent with the first prediction, 15 of 16 rats showed more suboptimal choice in the short-long condition compared to the short-short condition (left panel). However, all 16 rats showed *more* suboptimal choice in the long-long condition compared to the short-short condition (middle panel), which is inconsistent with the second prediction (because both short-short and long-long conditions generate an equal value for D_f/D_s). Finally, 15 of 16 rats showed *more* suboptimal choice in the extra-long-long condition than the short-short condition (right panel), which is inconsistent with the third prediction. Thus, there was little evidence at the individual subject level that longer IL durations offset the increase in suboptimal choice with longer delays to food. Instead, the vast majority of rats showed more suboptimal choice with relatively long delays to food at the choice point, regardless of the delay to temporally informative TL stimuli.

The top panel of Figure 5 depicts fits of the temporal information-theoretic model to data from the present experiment in addition to data from Cunningham & Shahan (2019). The purpose of combining data from each experiment was to gather as many data points as possible under conditions in which the temporal information-theoretic model makes a wide range of predictions (i.e., from suboptimal to optimal choice depending on condition). Relevant to the data analyzed here, the temporal information-theoretic model with the weighting mechanism defined by Equation 5 predicts 1) more suboptimal choice with larger values of D_f/D_s, and 2) the same degree of suboptimal choice in the short-short and long-long conditions (because they have the same value of D_f/D_s).

Cunningham & Shahan (2019) showed that the temporal information-theoretic model accurately described variations in suboptimal choice as TL duration, and therefore D_f/D_s, varied. However, when Equations 4 and 5 were fit to data from Cunningham & Shahan (2019) along with data from the present experiment, the model did not accurately describe suboptimal choice across the range of D_f/D_s values studied, accounting for only 59% of the variance (see top panel of Figure 5). This is not surprising given that results from the present experiment suggest that 1) suboptimal choice in rats is not sensitive to

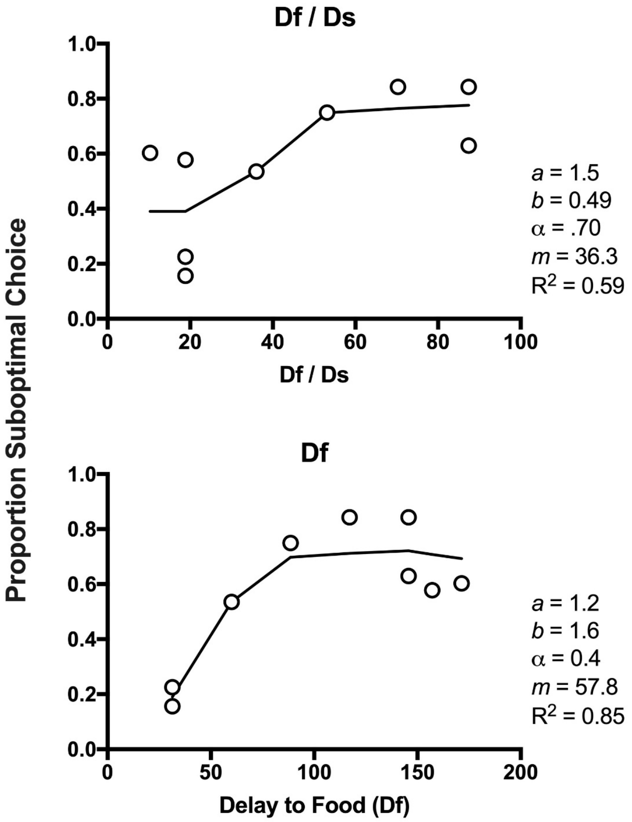

Figure 5. Top panel: fits of the temporal information-theoretic model (line) to obtained data (open circles) when the weighting mechanism is governed by D_f/D_s. Bottom panel: fits of the temporal information-theoretic model (line) to obtained data (open circles) when the weighting mechanism is governed by D_f.

D_s, and 2) suboptimal choice was not the same in the short-short and long-long conditions. This finding suggests that the weighting mechanism in rats is not influenced by the delay to temporally informative stimuli in general and is not governed by D_f/D_s in particular.

Although the delay to temporally informative TL stimuli does not appear to influence suboptimal choice in rats, results from the present experiment replicated the finding that longer delays to food at the choice point increase suboptimal choice. Perhaps a slight adjustment in the weighting mechanism, by replacing D_f/D_s with D_f, can do better. The bottom panel of Figure 5 shows the fit of the temporal information-theoretic model to data from the present experiment along with data from Cunningham & Shahan (2019) with the weighting mechanism defined by the equation below

$$w = \frac{1}{1 + e^{-\beta(D_f - m)}} \qquad (6).$$

The only difference between Equations 5 and 6 is that D_s is removed from Equation 6. The temporal information-theoretic model, with Equation 6 as the weighting mechanism, accounts for 85% of the variance[12]. Thus, one simple way to reconcile results from the present experiment with the temporal information-theoretic approach to suboptimal choice is to assume that the weighting mechanism is governed solely by the delay to food at the choice point in rats.

Discussion

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[12] Removing D_s from the weighting mechanism changes the interpretation of m. In Equation 4, m represents the unitless ratio, D_f/D_s, at which $w = 0.5$ In Equation 5, m represents the delay to food (in seconds) at which $w = 0.5$.

Research with both pigeons (e.g., Spetch et al., 1994; McDevitt et al., 2018) and rats (Cunningham & Shahan, 2019) has established a clear role for the delay to food (TL duration) in suboptimal choice. Both rats and pigeons require a relatively long delay to food at the choice point for food-predictive stimuli to entice them to select maladaptive actions, though rats appear to require a longer delay than pigeons. However, it is currently less clear if the delay to TL stimuli (i.e., IL duration) influences suboptimal choice. The present experiment was the first to assess the influence of IL duration on suboptimal choice in rats. We found that longer IL durations did not reduce suboptimal choice in rats, suggesting that suboptimal choice in rats is not affected by the delay to TL stimuli. These results have relevance to existing theories of suboptimal choice and might suggest a difference in the variables that govern suboptimal choice between rats and pigeons.

Previous research with pigeons suggests longer IL durations decrease suboptimal choice. However, this is based on only a few experiments (i.e., Experiment 3 from Dunn & Spetch, 1990; Kendall, 1974; Zentall et al., 2017), some of which have been criticized for unorthodox procedural details (e.g., the use of dark keys as TL stimuli in Kendall, 1974). Further, there is sometimes a high degree of individual variability in the influence of IL duration on suboptimal choice in pigeons (e.g., Zentall et al., 2017) and longer IL durations do not always decrease suboptimal choice (e.g., Experiment 1 from Dunn & Spetch, 1990). Given such limited and inconsistent evidence, some theories do not include a role for IL duration in suboptimal choice, such as the predictive-value hypothesis (Zentall, 2016) and the associability-decay model (Daniels & Sanabria, 2018). Other theories, however, suggest that IL duration plays a critical role in suboptimal choice. The signals for good news (SiGN) hypothesis (Dunn & Spetch, 1990; McDevitt et al., 2016) suggests that longer IL durations increase the conditioned-reinforcing value of TL stimuli for both suboptimal and optimal alternatives, eventually to the point where both have equal value. Once TL stimuli for each alternative have equal value (i.e., the value of TL stimuli are not pulling choice to one alternative or another), choice is no longer governed by the conditioned-reinforcing value of TL stimuli but is instead governed by the relative value of delayed food, which favors the optimal alternative. Thus, the SiGN hypothesis predicts less suboptimal choice with longer IL durations. Because we did not find reductions in suboptimal choice with longer IL durations, our results appear inconsistent with the SiGN hypothesis. However, it is difficult to draw precise predictions about how IL duration influences suboptimal choice according to the SiGN hypothesis because it is at present not formalized quantitatively. In this sense, it is not clear 1) the degree to which longer IL durations increase the value of TL stimuli, and 2) why differences in TL-stimulus value between alternatives should disappear as the overall value of TL stimuli for each alternative increases.

When viewed from the temporal information-theoretic approach, results from the present experiment suggest that Equation 5 (i.e., w governed by D_f/D_s) might not accurately describe the variables that govern competition between temporally informative stimuli and the rate of food delivery in rats. According to the Equation 5, increasing IL duration increases the delay to temporally informative TL stimuli at the choice point (D_s) and therefore decreases the weight given to relative temporal information as a determinant of choice. As a result, suboptimal choice should decrease as IL duration increases. Because longer IL durations did not reduce suboptimal choice in rats, results from the present experiment suggest rats and pigeons might need a different weighting mechanism. In particular, based on the limited data available, the weighting mechanism in pigeons is best described as a function of D_f/D_s (Equation 5) whereas the weighting mechanisms in rats might be best described as a function of D_f (Equation 6). As Figure 5 illustrates, defining the weighting mechanism for rats in terms of only the delay to food at choice point accounts reasonably well for data from the present experiment in addition to data from Cunningham & Shahan (2019)[13].

Changing the weighting mechanism for rats is only a post-hoc adjustment to illustrate how the temporal information-theoretic model might account for results from the present experiment. While it is possible that suboptimal choice in rats is simply not affected by IL duration (as Equation 6 assumes), this is by no means the only possibility. One possibility that has important implications for the temporal information-theoretic model relates to a procedural difference between the present experiment and previous research on suboptimal choice in pigeons.

The vast majority of research demonstrating less suboptimal choice with longer IL durations in pigeons arranged TL stimuli that conveyed the same amount of temporal information for each alternative (e.g., a choice between a suboptimal alternative

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[13] It is currently difficult to fit the temporal information-theoretic model to all suboptimal choice in rats as Cunningham & Shahan (2018) did with pigeons. The vast majority of research exploring suboptimal choice in rats used identical procedural parameters (e.g., a FR 1 IL schedule with 20% food for the suboptimal alternative and 50% for the optimal alternative). In addition, there are four different strains of rats (i.e., Long Evans, Sprague Dawley, Wistar, and Listar Hooded) represented in the nine published experiments on suboptimal choice in rats. Thus, the current data set on suboptimal choice in rats provides a very limited range of conditions for which the temporal information-theoretic model predicts different degrees of suboptimal choice, and the wide range of strains used make it difficult to find a single set of free parameters that works well for each strain

providing food 50% of the time with differential TL stimuli and an optimal alternative providing food 100% of the time). Under these conditions, the temporal information-theoretic model predicts indifference with short IL durations (when *w* is close to 1) because the temporal information conveyed by TL stimuli does not favor either alternative. As IL duration increases and *w* approaches 0, preference for the optimal alternative is expected. The procedure used in the present experiment differed from these previous experiments in that the food-predictive TL stimulus for the suboptimal alternative conveyed *more* temporal information than the TL stimulus for the optimal alternative. Under these conditions, the model predicts preference for the suboptimal alternative with short IL durations (when *w* is close to 1) and preference for the optimal alternative with longer IL durations (when *w* is close to 0). The fact that the present experiment arranged a more temporally informative TL stimulus for the suboptimal alternative should in no way affect the influence of IL duration on the weighting mechanism, and therefore suboptimal choice. Instead, having a more temporally informative TL stimulus for the suboptimal alternative only allows preference to shift to the suboptimal alternative as *w* approaches 1, rather than being capped at indifference as it is when TL stimuli convey the same amount of information. In other words, the temporal information-theoretic model suggests that the variables that govern the weighing mechanism (i.e., D_f and D_s) and relative temporal information do not interact to influence suboptimal choice.

It is possible, however, that the effect of IL duration on suboptimal choice in rats, and potentially pigeons, depends on the relative temporal information conveyed by TL stimuli. In other words, it is possible that IL duration interacts with relative temporal information in such a way that suboptimal choice varies with IL duration *only when TL stimuli are equally valued* (i.e., when temporal information does not pull choice towards one alternative or another). As discussed below, there is currently little evidence to address this issue, leaving it an open question for future research. However, the potential interaction between IL duration and relative temporal information (or relative TL value more generally) would violate a fundamental assumption of the temporal information-theoretic model that relative temporal information and the relative rate of food delivery do not interact with the variables that govern the weighting mechanism. As such, this is a critical issue for the temporal information-theoretic model because potential interactions between IL duration and relative temporal information would require a drastic restructuring of the model.

The only experiment to assess IL duration and suboptimal choice in pigeons when relative temporal information favored the suboptimal alternative was Zentall, Andrews & Case (2017). They assessed choice between a suboptimal alternative providing food 25% of the time with differential TL stimuli and an optimal alternative providing food 75% of the time without differential TL stimuli. Choice responses in the IL resulted in a transition to the TL according to either a fixed-interval (FI) 1 s schedule (i.e., short IL duration) or a FI 20 s schedule (i.e., long IL duration). Zentall et al., found less suboptimal choice in the long IL duration condition, suggesting that IL duration influences suboptimal choice in pigeons even when temporal information favors the suboptimal alternative (as it did in the present experiment). However, it is worth noting that there was a high degree of individual variability in suboptimal choice with long IL durations, with 2 of 5 pigeons showing near-exclusive preference for the optimal alternative and 3 of 5 pigeons showing some degree of preference for the suboptimal alternative.

In sum, it is currently unclear if the influence of IL duration on suboptimal choice interacts with the relative temporal information conveyed by (or relative value of) TL stimuli. While available data with pigeons shows that suboptimal choice decreases with longer IL durations when temporal information favors the suboptimal alternative, this conclusion rests on very limited data. Relevant data to address this issue in rats is even more limited given that the present experiment is the first to assess the influence of IL duration on suboptimal choice in rats. While we found that IL duration had no effect on suboptimal choice in rats, we did not have a condition in which temporal information conveyed by TL stimuli were the same for each alternative. A reasonable next step would be to assess suboptimal choice across a range of IL durations when TL stimuli for each alternative convey the same amount of temporal information. Future research addressing the possibility that IL duration interactions with the relative value of TL stimuli (in both rats and pigeons) will help draw more definitive conclusions about the role of IL duration in suboptimal choice. Such work will play an important role in guiding further developments in quantitative models of suboptimal choice in general, and the temporal information-theoretic model in particular.

If rats are indeed insensitive to IL duration regardless of the relative temporal information (or “value”) of TL stimuli, then it is important to address the question of why rats are not sensitive to IL duration. One possibility is that sensitivity to IL duration depends on the incentive salience of TL stimuli. Incentive salience refers to the attractive pull of food-predictive stimuli on behavior (Robinson & Berridge, 1993) and is measured by species-specific sign-tracking responses directed at food-predictive stimuli (e.g., a rat grabbing and chewing a lever that predicts food or a pigeon pecking an illuminated key that predicts food). The relation between incentive salience acquired by TL stimuli and suboptimal choice has been a centerpiece of research on suboptimal choice in rats (e.g., Chow et al., 2017; Lopez, Alba, & Orduna, 2018; Martinez et al., 2017; Zentall, Smith, & Beckmann, 2019). While it is currently unclear exactly how the incentive salience of TL stimuli influences suboptimal choice, there is a general consensus that incentive salience plays some role in suboptimal choice for both rats and pigeons. Evidence thus far suggests that incentive salience is neither necessary (Cunningham & Shahan, 2019; the present experiment) nor sufficient (Alba et al., 2018; Lopez et al., 2018; Martinez et al., 2017) for suboptimal choice in rats. However, it is possible that incentive salience plays a more subtle role in suboptimal choice.

Our experiment used a light-tone combination as TL stimuli, which do not acquire incentive salience in rats. In contrast, previous research that found an effect of IL duration on suboptimal choice in pigeons used lighted keys as TL stimuli, which do acquire incentive salience in pigeons. Perhaps sensitivity to the delay to TL stimuli (i.e., IL duration) depends its incentive salience. This possibility can be easily assessed by varying IL duration when either levers or lights are used for TL stimuli in rats. If sensitivity to the delay to TL stimuli depends on their incentive salience, then longer IL durations should decrease suboptimal choice only when levers, which typically acquire incentive salience in rats, serve as TL stimuli. Future studies addressing interactions between incentive salience and various parameters of the suboptimal choice procedure (e.g., IL and TL duration) might clarify the role incentive salience plays in suboptimal choice.

To summarize, results from the present experiment suggest that increasing the delay to temporally informative TL stimuli (via longer IL duration) does not affect suboptimal choice in rats. This result suggests that the weighting mechanism in rats is governed only by the delay to food at the choice point (D_f). Thus, results from the present experiment might suggest a difference in the variables that govern suboptimal choice between rats and pigeons. However, much more research is required to clarify 1) if and how IL duration influences suboptimal choice, and 2) if there are indeed differences in the potential role of IL duration on suboptimal choice between rats and pigeons.

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CHAPTER 5

GENERAL DISCUSSION

Despite evolutionary pressures that drive decision-making mechanisms in the direction of optimality (Stephen & Krebs, 1986), experimental studies on animal decision-making have revealed numerous maladaptive susceptibilities in decision-making processes (e.g., Fantino, 2012; Igaki, Romanowhich, & Sakagami, 2019; Zentall, 2014; 2019). Examples of maladaptive decision-making provide novel insights into the kinds of information animals use to make decisions along with the ways in which various sources of information compete and cooperate to control choice. As such, the study of maladaptive decision-making drives important theoretical and empirical developments within the decision-making literature. This paper explores one form of maladaptive decision-making, referred to as suboptimal choice, that is driven by the opportunity to earn stimuli that convey information about food. In particular, suboptimal choice reflects a phenomenon in which pigeons (at least) are willing to sacrifice food in order to earn food-predictive stimuli (i.e., stimuli that convey information about food).

Cunningham & Shahan (2018) proposed the temporal information-theoretic model as a way to understand suboptimal choice in pigeons. This model is based on the notions that 1) both food-predictive stimuli and food itself influence choice, 2) food-predictive stimuli influence choice based on the bits of temporal information they convey (Balsam & Gallistel, 2009; Balsam et al., 2010; Shahan & Cunningham, 2015), 3) food itself influences choice based on its delivery rate (Baum, 1974), and 4) temporal information and the rate of food delivery compete to control choice. This competition depends on a mechanism that assigns a weight (w) to relative temporal information and its complimentary weight (1-w) to the relative rate of food delivery as a determinant of choice. This weighting mechanism is governed by the delay to food (D_f) relative to the delay to temporal informative stimuli (D_s) at the choice point (i.e., D_f/D_s). When temporally informative stimuli are much closer in time than food itself, the temporal information conveyed by food-predictive stimuli holds more weight as a determinant of choice and suboptimal choice emerges. When temporally informative stimuli and food itself are both delayed, the relative rate of food delivery holds more weight as a determinant of choice and optimal choice is expected. Thus, the weighting mechanism describes the variables that govern competition between temporal information and the rate of food delivery as a determinant of choice. The temporal information-theoretic model accurately captures the vast majority of suboptimal choice data in pigeons by integrating two well-established ideas about what animals learn about food predictive stimuli that make them worth working for (Shahan & Cunningham, 2015) and how the rate of food delivery influences choice (Baum, 1974) into a single quantitative model.

Although suboptimal choice is a well-established phenomenon in pigeons, there is currently little evidence that rats also engage in suboptimal choice (Alba et al., 2018; Lopez, Alba, & Orduña, 2018; Martinez et al., 2017; Ojeda, Murphy, & Kacelnik, 2018; Trujano & Orduña, 2016; Trujano, López, Rojas-Leguizamón, & Orduña, 2016). Addressing potential species differences in suboptimal choice will clarify 1) the ubiquity with which food-predictive stimuli influence maladaptive decision-making, and 2) the generality of the temporal information-theoretic model as a framework for understanding the role of food-predictive stimuli in maladaptive decision-making. The novel weighting mechanism within the temporal information-theoretic model served as the centerpiece of our experiments exploring suboptimal choice in rats.

Of the three pieces of the temporal information-theoretic model, why should potential species differences in suboptimal choice lie in the weighting mechanism? First, it is unlikely that the influence of the relative rate of food delivery on choice differs between rats and pigeons. Indeed, the matching law is perhaps one of the most species-general and ubiquitous descriptions of choice among various sources of reinforcement (Davison & McCarthy, 1988). Thus, searching for potential species differences in the influence of the relative rate of food delivery on choice is unlikely to be a fruitful approach.

Second, the notion that animals learn about the temporal information conveyed by food-predictive stimuli is based on a long history of experiments on Pavlovian conditioning in both pigeons and rodents (for reviews, see Balsam et al., 2010; Gallistel & Gibbon, 2000). In addition, a ubiquitous assumption in the study of conditioned reinforcement is that Pavlovian conditioning governs the ability of food-predictive stimuli to maintain instrumental responding (e.g., Mackintosh, 1974; Shahan & Cunningham, 2015; Williams, 1994). There is little reason to believe that rats and pigeons differ in the processes that govern Pavlovian conditioning and therefore the ability of food-predictive stimuli to maintain instrumental responding. Thus, it is also unlikely that species differences in suboptimal choice are related to species differences in what animals learning about food-predictive stimuli that makes them serve as instrumental “conditioned reinforcers”.

Given ample evidence for the species-general role of temporal information in Pavlovian conditioning and the influence of the relative rate of food delivery on choice, a reasonable starting point to search for species differences within the temporal information-theoretic model is the (novel) weighting mechanism. Previous research on impulsive choice (i.e., preference for a sooner, smaller food over a later, larger food) has found that rats tolerate longer delays to food than pigeons before preferring a maladaptive alternative offering sooner, smaller food (Green et al., 2004; Mazur, 2000; Mazur & Biondi, 2009; Tobin & Logue, 1994). A natural extension of species differences in sensitivity to delayed food to the temporal information-theoretic model is to assume that rats and pigeons differ in the value of D_f/D_s that is sufficiently large generate suboptimal choice (via increases in w). Perhaps rats require a longer delay to food, and therefore a larger value of D_f/D_s, before basing decisions on relative temporal information and therefore engaging in suboptimal choice.

Cunningham & Shahan (2019; see Chapter 3) showed that longer delays to food increased suboptimal choice in rats as it does in pigeons. However, results from Cunningham & Shahan (2019) left open the question of whether the delay to food *relative to* temporally informative stimuli (i.e., D_f/D_s) is critical in rats, or if just the delay to food (i.e., D_f) matters. The weighting mechanism is governed by D_f/D_s, and not just D_f, because limited evidence in pigeons suggests that longer delays to temporally informative stimuli (i.e., D_s) decreases suboptimal choice. To address the role of D_s in suboptimal choice in rats, we conducted an experiment (reported in Chapter 4) in which the delay to temporally informative stimuli varied across conditions. As a result of the current formulation of the weighting mechanism, the temporal information-theoretic model predicts that suboptimal choice should decrease as the delay to temporally informative stimuli increases, effectively offsetting the increase in suboptimal choice with long delays to food. However, results from our experiment suggested that suboptimal choice in rats is insensitive to the delay to temporally informative stimuli. Thus, these results suggest a potential difference in the variables that govern suboptimal choice between rats and pigeons. Limited evidence suggests that pigeons are sensitive to the delay to temporally informative stimuli at the choice point whereas rats are not.

A simple way to account for this potential species differences within the temporal information-theoretic model is to assume that the weighting mechanism is governed by different variables in rats and pigeons. When the temporal information-theoretic model with D_f/D_s governing the weighting mechanism was fit to data from our two experiments, the model accounted for only 59% of the variance. The model systematically underpredicted suboptimal choice with long IL durations in addition to predicting the same degree of suboptimal choice in conditions with the same value of D_f/D_s (which is inconsistent with results from the experiment reported in Chapter 4). However, when the model is fit to the same data but with the weighting mechanism governed by D_f, the model accounted for 85% of the variance, without any systematic deviations from obtained data. Thus, evidence collected from our two experiments suggest that the weighting mechanism in rats is governed only by D_f. However, this is only a tentative conclusion given the limited data on which it is based.

Given uncertainty about the influence of delayed temporally informative stimuli on suboptimal choice in pigeons (i.e., Kendall, 1974; Dunn & Spetch, 1990; Zentall et al., 2017), perhaps the temporal information-theoretic model can still do reasonably well with the weighting mechanism governed only by D_f when applied to pigeon data. When the weighting mechanism is governed by just D_f for pigeons, the model accounts for only 62% of variance in the data, systematically overpredicting suboptimal choice for experiments with relatively long delays to temporally informative stimuli and failing to capture variations in suboptimal choice in experiments directly manipulating the delay to temporally informative stimuli. Thus, the temporal information-theoretic model suffers problems when the weighting mechanism is governed solely by D_f for pigeons. For this reason, available evidence suggests that the weighting mechanism needs to be different between rats and pigeons. However, it is important to note that much more research is needed to clarify 1) if and how delays to temporally informative stimuli influence suboptimal choice, and 2) if there are indeed differences between rats and pigeons in the influence of delays to temporally informative stimuli on suboptimal choice.

While experiments reported in Chapters 3 and 4 address suboptimal choice in rats in terms of the weighting mechanism, many unanswered questions remain about the processes that govern suboptimal choice in rats (and its potential differences with pigeons). One of the most striking features of suboptimal choice in pigeons is that choice appears to be completely insensitive to reductions in the rate of food delivery for the suboptimal alternative. Provided that the suboptimal alternative offers stimuli that signal probabilistic food, pigeons prefer the suboptimal alternative even when the optimal alternative provides 35 times more food (Fortes, Vasconcelos, & Machado, 2016). Now that we can generate suboptimal choice in rats (via increases in the delay to food), it would be interesting to see if rats, like pigeons, are insensitive to drastic reductions in the rate of food delivery for the suboptimal alternative. According to the temporal information-theoretic model, as long as *w* is close to one, variations in the rate of food delivery for the suboptimal alternative should have, at most, a minimal effect on suboptimal choice.

It would also be worthwhile to address questions related to the role of incentive salience in rodent suboptimal choice. Incentive salience refers to the attractive, "magnetic" pull of food-predictive stimuli on behavior and has been implicated in a wide array of maladaptive forms of decision-making (see Flagel, Akil, & Robinson, 2009; Robinson & Berridge, 1993). Chow et al., (2017) suggested that the use of levers as food-predictive stimuli, which acquire incentive salience when correlated with food delivery, would generate suboptimal choice in rats. Consistent with this notion, Chow et al., (2017) found more suboptimal choice in rats when post-choice stimuli were levers compared to lights. However, numerous experiments have since failed to find suboptimal choice in rats when levers were used as post-choice stimuli (Alba et al., 2018; Lopez et al., 2018; Martinez et al., 2017). Thus, current evidence suggests that incentive salience is not sufficient for suboptimal choice in rats. Further, Cunningham & Shahan (2019), along with data presented in Chapter 4, found suboptimal choice in rats when a light-tone combination (which does not acquire incentive salience) was used for post-choice stimuli, suggesting incentive salience is also not necessary for suboptimal choice in rats.

It is possible, however, that incentive salience plays a more subtle role in suboptimal choice, though it is not clear exactly what that role is. Within the temporal information-theoretic model, the role of incentive salience might influence the free parameters of the weighting mechanism, thereby modulating the influence of D_f, or D_f/D_s, on the weight given to temporally informative stimuli on choice. For example, perhaps incentive salience reduces the delay to food required to induce suboptimal choice in rats. This possibility could easily be assessed by replicating the experiment from Chapter 3 but with the use of levers as post-choice stimuli and comparing the function relating suboptimal choice to delayed food when post-choice stimuli have (levers) or do not have (light + tone) incentive salience. Further, it is possible that post-choice stimuli with incentive salience encourage rats to consider the delay to temporally informative stimuli when making decisions. Perhaps if we replicated the experiment from Chapter 4 with levers as post-choice stimuli, increasing the delay to temporally informative stimuli would reduce suboptimal choice in rats as it appears to in pigeons. Regardless of the details, further exploring the role of incentive salience in suboptimal choice will help situate the phenomenon within the larger framework of maladaptive, clinically relevant behavior induced by food-predictive stimuli that have acquired incentive salience.

In summary, this project illustrated the value of using quantitative models with well-defined concepts to 1) understand the processes by which animals make maladaptive decisions, and 2) inform experimentation to address relevant issues in the study of maladaptive decision-making. In this case, we used the temporal information-theoretic model as a vehicle for exploring suboptimal choice in rats. This approach revealed novel insights into the conditions in which rats engage in suboptimal choice and how these conditions differ from those in which pigeons engage in suboptimal choice.

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Zentall, T. R., Andrews, D. M., & Case, J. P. (2017). Prior commitment: its effect on suboptimal choice in a gambling-like task. *Behavioural Processes*, 145, 1-9.

CURRICULUM VITAE

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EDUCATION

2008 - 2013
B.S. Psychology (Graduate Preparation)
Central Michigan University – Mt. Pleasant, MI

B.A. Philosophy
Central Michigan University – Mt. Pleasant, MI

2013 - Present
Ph.D. Psychology – In Progress
Utah State University – Logan, UT

RESEARCH EXPERIENCE

2013 – Present
Graduate Student Research: Experimental and Applied Psychological Sciences, Utah State University (advisor: Dr. Timothy Shahan).
2012 – 2013
Undergraduate Student Research: Experimental Psychology – Brain and Behavior, Central Michigan University (advisor: Dr. Mark P. Reilly).
2011 – 2013
Undergraduate Student Research: Experimental Psychology – Social/Personality/Evolutionary, Central Michigan University (advisor: Dr. Melvin Jaffa).

TEACHING EXPERIENCE

Spring 2014
Graduate Teaching Assistant, Utah State University
Course: Neuroscience I
Primary Instructor: Catalin Buhusi

- Fall 2014 – Spring 2015
  - Graduate Teaching Assistant, Utah State University
  - Course: Basic Behavioral Processes (Lab Section)
  - Primary Instructor: Gregory Madden
- Fall 2016 – Spring 2017
  - Graduate Teaching Assistant, Utah State University
  - Course: Basic Behavioral Processes (Lecture Section)
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Instructor, Utah State University
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Instructor, Utah State University
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PROFESSIONAL ASSOCIATIONS

2012-2013
Behavior Analysis Association of Michigan, Student Member

2012-2013
Mid-American Association of Behavior Analysis, Student Member

2012-Present
Association for Behavior Analysis, Student Member

2013-Present
Society for the Quantitative Analysis of Behavior, Student Member

EDITORIAL ACTIVITIES

Post-Hoc Reviewer For:
Journal of the Experimental Analysis of Behavior
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PUBLICATIONS

Shahan, T. A., & Cunningham, P. J. (2015). Conditioned reinforcement and information theory revisited. *Journal of the Experimental Analysis of Behavior,* 103, 405-418.

Craig, A. R., Cunningham, P. J., & Shahan, T. A. (2015). Behavioral momentum and accumulation of mass in multiple schedules. *Journal of the Experimental Analysis of Behavior,* 103, 437-449.

Cunningham, P. J., Kuhn, R., & Reilly, M. P. (2015). A within-subject, between-apparatus comparison of impulsive choice: T-maze and 2-lever chamber. *Journal of the Experimental Analysis of Behavior,* 104, 20-29.

Nevin, J. A., Craig, A. R., Cunningham, P. J., Podlesnik, C. A., Shahan, T. A., & Sweeney, M. M. (2017). Quantitative models of persistence and relapse from the perspective of behavioral momentum theory: Fits and misfits. *Behavioural Processes*, 141, 92-99.

Craig, A. R., Cunningham, P. J., Sweeney, M. M., Shahan, T. A., & Nevin, J. A. (2018). Delivering alternative reinforcement in a distinct context reduces its contra-theraputic effects on relapse. *Journal of the Experimental Analysis of Behavior,* 109, 492-505.

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CONFERENCE PRESENTATIONS

Cunningham, P. J., Craig, A. R., Fihlo, P. S., & Shahan, T. A. (2015, May). *Observing, conditioned reinforcement, and temporal information*. Presented at the Association of Behavior Analysis International Annual Conference, San Antonio, TX.

POSTER PRESENTATIONS

Cunningham, P. J., & Jaffa, M. (2012, April*). Belief in Free Will and Cognitive Dissonance.* Poster presented at SCREE 2012 poster session at Central Michigan University.

Brooks, M. A., Cunningham, P. J., Reilly, M. P. (2013, February). *Progressive-Ratio Schedules and Drug Self-Administration: A Follow up to Stafford, LeSage, & Glowa (1998).* Poster presented at Behavior Analysis Association of Michigan Annual Conference, Ypsilanti, MI.

Cunningham, P. J., Reilly, M. P. (2013, May). *Resistance to Extinction When an Alternative Response is Reinforced: Deviations from Momentum Theory?* Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, Minneapolis, MN.

Cunningham, P. J., Kuhn, R. M., Reilly, M. P. (2014, April). *A Comparison of Impulsive Choice Using a T-maze and a Standard Operant Chamber.* Poster presented at SCREE 2014 poster session at Central Michigan University.

Nall, R. W., Craig, C. R., Cunningham, P. J., Marshall, C., Shahan, T. A. (2014, April). *Duration of Extinction is Negatively Related to Resurgence of Ethanol Seeking Following Loss of Non-Drug Alternative Reinforcement in Rats.* Poster presented at Four Corners Association for Behavior Analysis Annual Conference, Park City, UT.

Cunningham, P. J., Filho, P. S., Craig, A. R. (2014, May). *Conditioned Reinforcement and Informativeness Reconsidered*. Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, Chicago, IL.

Kuhn, R. M., Cunningham, P. J., Reilly, M. P. (2014, May). *Behavioral Momentum in Mixed and Multiple Schedules of Reinforcement.* Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, Chicago, IL.

Nelson, S. A., Craig, A. R., Nall, R. W., Cunningham, P. J., Frye, C. C. J., & Shahan, T. A. (2015, May). *Resurgence of alcohol seeking: Effects of length of exposure to extinction plus alternative reinforcement*. Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, San Antonio, TX.

House, K. O., Craig, A. R., Cunningham, P. J., & Shahan, T. A. (2015, May). *Differences in resistance to extinction between single and multiple schedules may be related to testing conditions*. Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, San Antonio, TX.

Cunningham, P. J., & Shahan, T. A. (2016). *Arousal and resistance to change in multiple schedules.* Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, Chicago, IL.

Cunningham, P. J., & Shahan, T. A. (2017). *Exploring the role of temporal information in suboptimal choice*. Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, Denver, CO.

Cunningham, P. J., & Shahan, T. A. (2018). *Conditioned reinforcement is sensitive to reinforcer devaluation.* Poster presented at Society for the Quantitative Analysis of Behavior Annual Conference, San Diego, CA.

RESEARCH GRANTS

SCREE 2012 Undergraduate Research Grant: “Differential Effects of the Apparatus Used to Study Impulsive Choice: A Comparison Between a T-Maze and an Operant Chamber”, $500 (November, 2012-2013*)*.

Utah State University Psychology Dissertation Award: “Exploring Suboptimal Choice in Rats Using the Temporal information-Theoretic Model”, $2,000 (December, 2018-2019)