Universidade do Minho
Escola de Psicologia

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Biasing Temporal Performance of Pigeons and Humans

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Biasing Temporal Performance of Pigeons and Humans

Tese de Doutoramento
em Psicologia Básica

Trabalho efetuado sob a orientação do
Professor Doutor Armando Machado

e do
Professor Doutor Marco Vasconcelos

Março de 2019

STATEMENT OF INTEGRITY

I hereby declare having conducted my thesis with integrity. I confirm that I have not used plagiarism or any form of falsification of results in the process of the thesis elaboration. I further declare that I have fully acknowledged the Code of Ethical Conduct of the University of Minho.

University of Minho, March 28th, 2019.

Full name: Renata Penna Borges Nunes Cambraia

Signature:

Renata Cambraia

“In general, a time filled with varied and interesting experiences seems short in passing, but long as we look back. On the other hand, a tract of time empty of experiences seems long in passing, but in retrospect short”.

— William James, 1890.

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BIASING TEMPORAL PERFORMANCE OF PIGEONS AND HUMANS

Interval timing pertains to the ability of organisms to adapt their behavior to the temporal regularity of stimuli such as lights, sounds, or food. Although a set of properties have been established to characterize timing, researchers will encounter phenomena such as temporal distortions, or biases. That is, temporally controlled behaviors may be sensitive to non-temporal variables, such as payoffs (reinforcement probabilities) and base-rates (frequency of stimulus intervals). How timing is affected by these variables in different tasks and species is debatable. In the present dissertation, we discuss these issues throughout four studies investigating how payoff and base-rate affect pigeons and humans in a temporal bisection task. This temporal discrimination task is tested in its standard version – subjects choose one arbitrary key after a short interval sample and another after a long sample (e.g., short—green, long—red) – and a novel version – subjects choose based on location (e.g., short—left, long—right), and their motion is recorded throughout the intervals. While pigeons were placed in either a standard or long operant chamber, human participants were exposed to a standard computer task or a game that required them to move a spaceship horizontally and shoot one of the two aliens at the top corners of the screen. All subjects learned the task and produced a psychometric function (i.e., proportion of "long" responses), characterized by a location (bias) and a scale (sensitivity) parameter. After learning the task, subjects each went through three experimental conditions: Long-Bias, No-Bias, and Short-Bias, indicating the expected effects from the base-rate and payoff manipulations. In general, while bias effects (horizontal shifts of the psychometric functions) were consistent, no significant change was observed in sensitivity to the intervals. The novel task produced stereotypical motion patterns during baseline training – on the long sample trials, subjects approached the short key after sample onset, stayed there for some time, then departed to the long key. During the manipulations, new patterns emerged, especially for the pigeons, and motion was no longer always a good predictor of the proportion of "long". These results contribute to our understanding of the basic mechanisms involved in interval timing and learning and challenge current timing models to account for competition of stimulus control and new measures of temporal performance, such as motion.

ENVIESANDO O DESEMPENHO TEMPORAL DE POMBOS E HUMANOS

A perceção temporal intervalar se refere à habilidade dos organismos em adaptarem seu comportamento à regularidade temporal de estímulos como luzes, sons, ou comida. Apesar de uma série de propriedades terem sido estabelecidas para characterizar a perceção temporal, pesquisadores encontrarão fenômenos como distorções, ou viéses, temporais. Isto é, comportamentos temporalmente controlados podem ser sensíveis a variáveis não temporais, como ganhos (*payoffs*; probabilidades de reforço) e taxas-base (*base-rates*; frequencia dos estímulos). Como a perceção temporal é afectada por essas variáveis é debatível. Na presente tese, discutimos esses temas através de quatro estudos que investigam como ganhos e taxas-base afetam pombos e humanos em uma tarefa de bisecção. Essa tarefa de discriminação temporal é testada em sua versão padrão – os sujeitos escolhem uma chave após um intervalo curto e outra após um intervalo longo (e.g., curto—verde, longo—vermelho) – e uma versão nova – os sujeitos fazem escolhas baseadas em localização (e.g., curto—esquerda, longo—direita), e seu movimento é registrado durante os intervalos. Enquanto os pombos eram colocados em uma caixa operante padrão ou em uma caixa longa, participantes humanos foram expostos a uma tarefa de computador padrão ou um jogo que exigia que movessem uma nave espacial horizontalmente e atirassem em um dos dois extraterrestres nos cantos superiores do ecrã. Todos os sujeitos aprenderam a tarega e produziram funções psicométricas (i.e., proporção de respostas “longo”), caracterizadas por um parâmetro de localização (viés) e um de escala (viés). Após aprender a tarefa, cada sujeito foi exposto a três condições experimentais: Viés-Longo, Sem-Nenhum e Viés-Curto, que indicam os efeitos experados das manipulações de ganhos e taxas-base. Em geral, enquanto efeitos de viés (deslocação horizontal da função psicométrica) foram consistentes, não houve mudanças significativas na sensibilidade aos intervalos de tempo. A nova tarefa produziu padrões de movimento esteriotipados durante o treino da linha de base – nos ensaios com duração longa, os sujeitos se aproximaram à chave curta após o início do intervalo, permaneceram ali por algum tempo, então partiram para a chave longa. Durante as manipulações apareceram novos padrões, especialmente nos pombos, e o movimento já não era sempre um bom preditor da proporção de “longo”. Esses resultados contribuem com a nossa compreensão dos mecanismos básicos envolvidos na perceção temporal intervalar e na aprendizagem, e desafiam modelos atuais a considerar a competição por controle de estímulos e novas medidas de desempenho temporal, como padrões de movimento.

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ABBREVIATIONS, ACRONYMS AND SYMBOLS

ANOVA – Analysis of Variance

AT – Arrival Time

Δ – Payoff differential

α – Alpha; Lower asymptote parameter

β – Beta; Upper asymptote parameter

DT – Departure Time

ECDF – Empirical Cumulative Distribution Function

FI – Fixed Interval schedule

FOPP – Free-operant Psychophysical Procedure

ITI – Intertrial Interval

L – Long duration

L – Straight to long motion pattern

λ – Location in operant chamber

LB – Long Bias

μ – Miu; Mean, or location parameter

NB – No Bias

O – Overall probability of reinforcement

p – Proportion of short baited trials

PSE – Point of Subjective Equality

q – Proportion of long baited trials

r – Proportion of long trials

s – Proportion of short trials

S – Short duration

S – Only short motion pattern

SS – Short → short motion pattern

SL – Short → long motion pattern

σ – Standard deviation, or scale parameter

SB – Short Bias

t – Time

VI – Variable Interval schedule

VR – Variable Ratio schedule

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CHAPTER I

INTRODUCTION

In this chapter I will briefly review the main topics imbued in this dissertation. It begins by describing what interval timing is and how this area came about. I will also characterize the behavioral approach used in this work to study the temporally controlled behaviors of human and non-human animals. I will illustrate the main task used to study timing in this dissertation: the temporal bisection task, and its typical results and interpretations; as well as propose using a novel version of the task to improve our knowledge on ongoing processes during timing of the presented interval cues. Then, I will explore the sub-field of temporal distortions and how the modified version of the bisection task can help us understand how important environmental variables, namely base-rates and payoffs, can bias temporally controlled behaviors. I will briefly discuss two leading timing models and how they could shed light on the underlying processes of how timing behavior is affected by non-temporal variables. Finally, I convey our approach towards a comparative psychology of timing, and finish with the objectives for this dissertation and how they will be addressed in the following chapters.

Interval Timing

Time is a ubiquitous and dynamic dimension of environmental events that has been an intensive focus of both theory and research. The study of behavior under control of temporal aspects of the environment is usually separated into two broad categories (Shettleworth, 2010). Circadian timing pertains to behavior entrained in the light and dark daily periods of *circa* 24 h (e.g., eating, sleeping). Interval timing relates to the ability of an organism to adapt its behavior to the temporal regularity of stimuli such as lights, sounds, or food in a shorter time range (Church, 2002b; Shettleworth, 2010). Since as early as the 19th century, this growing area of research has been demonstrating the accuracy with which humans and non-human animals are able to estimate very short intervals of time, from milliseconds to hours (James, 1890).

As senses such as sight and hearing are sustained by dedicated organs, early speculations assumed that there must be some physical organ in the human body directly responsible for timing. Because organisms can adequately and adaptively respond to the passage of time without precise external cues, i.e., a "clock", it is often hypothesized that they must have some sort of internal mechanism enabling them to respond correctly. Treisman (1963), for example, proposed the idea of an internal, biological clock in human psychophysics. John Gibbon (1977) further developed the idea of a pacemaker-accumulator clock and applied it to animal experiments. Gibbon's contributions (for a review, see Church, 2002a) were essential in developing the area of interval timing. In fact, he formulated a cognitive model (Scalar Expectancy Theory, SET; Church & Gibbon, 1982; Gibbon, 1977) that is still the main approach to timing in psychology (there are a number of other approaches, especially in neuroscience, e.g., Buhusi & Meck, 2005). However, this approach often over-emphasizes internal properties of the timing process while de-emphasizing environmental causes. It is also concerned with steady-state behavior and not with issues of learning, such as how animals learn to time and how the timing mechanisms are affected by learning.

A Behavioral Approach to Timing

The study of the temporal control of behavior appeared as early as in Pavlov's experiments on respondent conditioning and inhibition of delay (e.g., Pavlov, 1927) and was further pursued in Skinners' work on interval schedules of reinforcement (e.g., Ferster & Skinner, 1957; Skinner, 1938). This early work by Skinner influenced the field of interval timing by contributing with methodological advances in the study of animal timing as well as theoretical advances in the way we understand time (for reviews, see Lejeune, Richelle, & Wearden, 2006; Zeiler, 1977). Nonetheless, behaviorists only took special interest in researching interval timing with the study of "time markers", or biologically relevant stimuli that signal that an interval has started, or ended, and evoke temporally correlated behavior (e.g., Staddon & Innis, 1966, 1969; Staddon, Wynne, & Higa, 1991). This approach emphasizes that timing behavior must be cued by some aspect of the environment (Staddon & Cerutti, 2003).

However, time still differs in fundamental and interesting ways from other environmental cues, such as space and number, which establish (at least apparently) relations between palpable objects. Time can be extremely difficult to define and, since there is no obvious exteroceptive stimulus or mediating receptor (Gibson, 1975), it is arguably a stimulus in itself (Staddon & Cerutti, 2003; but see Mcmillan, Spetch, Sturdy, & Roberts, 2017). Alternatively, time can also be conceived as another stimulus dimension (J. Gregor Fetterman, 1996), along with many others, such as brightness or loudness, which have been typically manipulated in early studies on stimulus control (Terrace, 1966).

In any case, this dissertation adopts a behavioral approach to timing and will articulate the effects of environmental stimuli on behavior, under a perspective of stimulus control, moving away from, but not ignoring, internal explanations involving hypothetical constructs such as internal clocks (Eckard & Lattal, 2019). From the early works of Pavlov and Skinner, it took a few decades until the first attempts to model time-controlled behavior under a behavioral approach (Behavioral Theory of Timing, BeT; Killeen & Fetterman, 1988). Current developments include the Behavioral Economic Model (BEM; Jozefowiez, Staddon, & Cerutti, 2009) and Learning-to-Time (LeT; Machado, 1997b; Machado, Malheiro, & Erlhagen, 2009), which incorporate associative learning processes. Despite the differences in the wide array of models existing today, they all tend to account for a set of basic properties of interval timing.

The Scalar Property

Since the early studies, a considerable amount of data has been collected, which allowed the identification of set of properties of interval timing (Church, 2002b; Gibbon, 1977). Perhaps the most pervasive is the scalar property – a proportion of the maximum response rate occurs at a proportion of the stimulus interval. To illustrate, picture a rat pressing a lever (R_1) during a fixed interval (FI) 30 s schedule of reinforcement. Response rate increases from $t = 0$ s, as a function of time, reaching its maximum at $t = 30$ s. If you now require the animal to respond on a FI 90 s schedule (R_2) and plot both functions in a relative scale, they superimpose, i.e., $R_1(t/3)$ is proportional to $R_2(t)$.

Thus, the standard deviation of the measured behavioral variable should increase linearly with its mean, yielding a nearly-constant *coefficient of variation*. In other words, the scalar property means that timing accuracy (as defined by the coefficient of variation) remains constant across time. This is the equivalent of Weber's law applied to the time domain. It is important to note, however, that the generality of this and other properties has not ceased to be debated (Staddon & Cerutti, 2003; J. H. Wearden & Lejeune, 2006), since deviations continue to be found (e.g., Bizo, Chu, Sanabria, & Killeen, 2006).

The Temporal Bisection Task

A variety of procedures have been developed to study timing since the fixed-interval reinforcement schedule (Skinner, 1938). In particular, the temporal bisection task (Church & Deluty, 1977; Platt & Davis, 1983) has been very popular in the timing literature, especially since the procedure was easily replicated with humans (J. H. Wearden, 1991). In this task (Figure 1), a sample stimulus is presented for a specific time interval after which two manipulanda are presented. Subjects are then required to choose the corresponding option: one response is correct after short durations, say 3 s, (e.g., pecking red) and the other is correct after long durations, say 9 s (e.g., pecking green). Correct responses are reinforced with grain and incorrect responses are not reinforced; instead, the chamber goes dark and an intertrial interval (ITI) is initiated. When subjects discriminate the two intervals (i.e., they learn to peck red after a short sample and green after a long sample), they are presented with intermediate sample durations and their preference for one of the keys is measured.

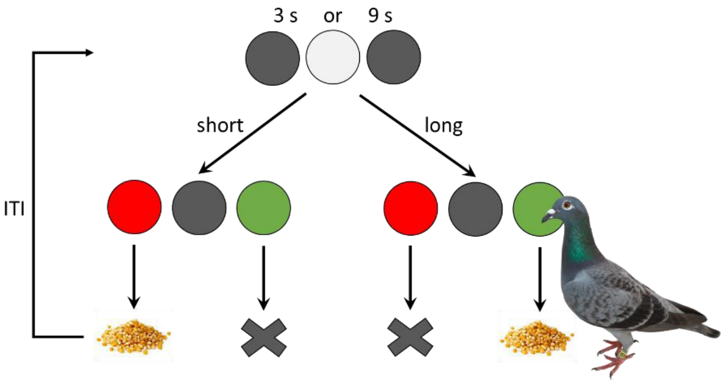

Figure 1. Structure of a temporal bisection task with pigeons. Each trial begins with the center key illuminating for 3 s or 9 s (sample stimulus); at sample offset, the side keys turn red or green (choice options); correct responses are reinforced with access to grain, incorrect responses lead straight to the intertrial interval (ITI).

This task is especially relevant in the study of temporal discrimination because an important set of parameters, components of a four-term operant contingency (Sidman, 2008) – the sample (conditional stimulus), the response keys (antecedent stimuli), pecking (response), and the food reward (consequence) – may be varied independently to produce subsequent behavioral changes.

The Psychometric Function and its Interpretations

Results from the temporal bisection task are typically plotted as proportion of “long” responses (in my example, the responses on the green key) as a function of sample duration, also referred to as a psychometric function (Church & Deluty, 1977; Stubbs, 1968). Typically, this function (Figure 2A) increases as the sample duration increases, approximately from zero to one. The indifference point (μ) – the duration (x-axis) corresponding to the halfway point of the function (y-axis) – is often referred to as the point of subjective equality, or PSE, and is considered the subjective middle because “short” responses are just as likely as “long”. The slope (σ) of the function at μ indicates sensitivity to the presented intervals. The upper and lower asymptotes (α and β) indicate the proportion of “long” for the short and long samples, respectively. The psychometric function tends to obey the scalar property – when different sample pairs of constant ratios are used, the functions superimpose when plotted in relative rather than absolute time.

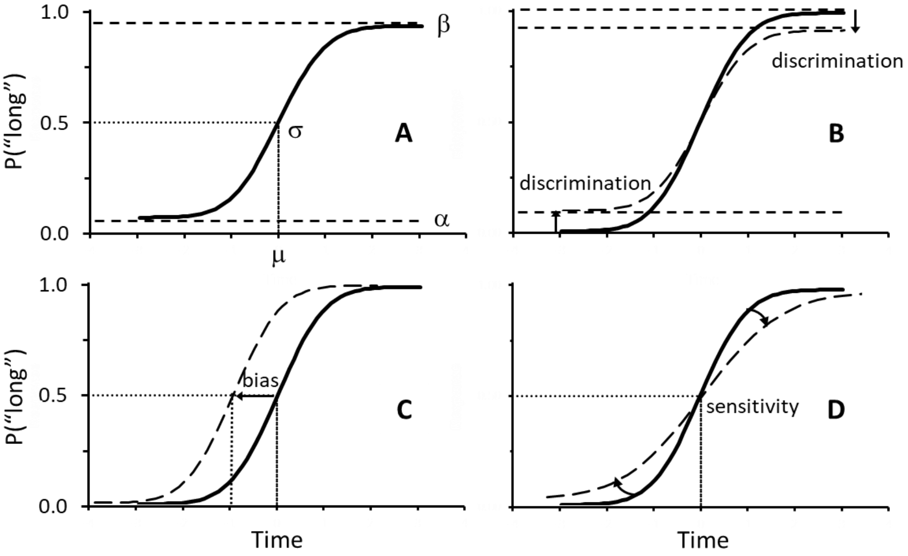

Figure 2. The psychometric function and possible effects of manipulations on contingencies in the temporal bisection task. A) Parameters: location, scale, lower asymptote, upper asymptote. B) Loss of discrimination at the anchors (trained samples). C) Leftward shift in location, i.e., bias towards "long" responses. D) Flattening of the function, i.e., decrease in sensitivity to time.

These function parameters can be affected by different manipulations of the temporal bisection task. Each effect can be interpreted in "psychological" terms, or what it would mean in terms of the subjective perception of time (Allan, 2002; Blough, 1996). For instance, changes in the asymptotes (Figure 2B), away from zero at the short duration and from one at the long duration, indicate loss of discrimination of the trained samples. Because these are considered errors for supposedly learned duration–response associations, they are often interpreted as a loss in "attention"; however, attention can have many meanings and errors are not necessarily due to lack of attention (Blough, 1996). Bias is a measure of preference for a response, which will produce shifts along the duration axis (i.e., the x-axis) of the function and is represented by an increase or decrease in parameter μ. A bias to respond on the "long" key during the presentation of intermediate samples moves the response function to the left and decreases the PSE (Figure 2C). Conversely, a bias to respond on the "short" key moves the psychometric function to the right and increases the PSE (Gibbon, 1981). Although response and perceptual bias may be indistinguishable in a bisection task (Raslear, 1985), the typical interpretation is that bias indicates that the passage of time subjectively feels "slower" or "faster"— a perceptual bias. A horizontal flattening of the psychometric function (Figure 2D) indicates loss of overall temporal control, also referred to as a loss in sensitivity to time.

A completely horizontal function indicates that the animal behaves similarly to all the presented sample intervals and is thus not timing the stimuli (i.e., is “indifferent”). Conversely, a steep function indicates a discrimination between each presented interval and its adjacent intervals and thus the temporal perception of the subject is precise.

The temporal bisection is sometimes referred to as a matching-to-sample task because the subject must choose, or match, a response that corresponds to the sample, the only difference being the nature of the stimulus (temporal), and falls under the category of choice procedures. However, the assumption underlying choice behavior in this task is that the actual “decision” of which response to emit was made sometime during sample presentation; for the long sample, it would be after the time elapsed has lasted well past the short interval. Further, the subject cannot determine which interval will be presented at sample onset, but certainty would increase with time (picture a fixed-interval schedule scalloped pattern of responding) – representing the dynamic property of temporal events. For example, Akdoğan & Balcı (2016a) found that response times were faster for the long duration, probably because the decision was made before sample offset. Thus, a major setback of the typical bisection task is the lack of information regarding the subject’s behavior throughout the to-be-timed interval.

A Novel Bisection Task

Machado and Keen (2003) conceived a version of the temporal bisection task that would enable tracking behavior during the samples and correlate it to the choice after sample offset. In a sense, they “externalized” hypothetical ongoing timing processes that are not observable in a typical choice procedure. To do so, instead of the typical arbitrary duration—color key relation, pigeons learned a duration—location mapping. In a sense, this is similar to the version of the bisection task used with rodents (e.g., 2 s—left lever, 8 s—right lever, Church & Deluty, 1977), but with keys placed far apart in a longer-than-usual operant chamber. Floor panels enable recording pigeons’ location in time, i.e., their motion patterns.

Initially, pigeons remained oriented towards the center key that initiated the trial but, as training progressed, the birds learned a particular motion pattern that became highly stereotypical by the end of training. At long sample onset, they moved to the *short* (left) side of the chamber, remained past the duration of the short sample, and then departed to the *long* (right) side. This steady-state behavior translated into three dependent variables, all measured at the *short* side: arrival time, departure time, and residence time (arrival – departure). The departure time is especially relevant because the moment the bird leaves the short side may be considered a criterion separating the short and long intervals. In other words, it could be considered as the moment the subject decides that the sample is not short, but long (viz., "short-no-short hypothesis") and thus a good approximation of the PSE. Machado and Keen (2003) showed this to be the case, and the empirical cumulative distribution of these departure times were a good approximation of the proportion of "long" choices (i.e., the psychometric function). Further, these parameters obeyed the scalar property.

Showing that these measures are equivalent is an advancement in the study of interval timing in a number of ways. First of all, it enables to better understand the evolution of the learning process of the temporal discrimination, and not only steady-state behavior. We can observe, for example, how the psychometric function and the PSE change with training, including the mean and standard deviation parameters (and the scalar property).

Secondly, although the temporal bisection is a widely used task, obtaining information as simple as the PSE requires extensive testing, since measuring proportion relies on plenty of trials with a range of different durations to obtain reliable data. However, this duration—location adaptation of the task enables observing an equivalent to the PSE, i.e., the departure time, for every long trial.

Thirdly, the fact that we can learn about the ongoing decision process during the sample approximates the bisection task to other popular interval timing procedures. While the standard bisection obtains response measures after the to-be-timed interval, tasks such as the peak procedure (Catania, 1970; Roberts, 1981) or the free-operant psychophysical procedure (Stubbs, 1980) observe ongoing timing by measuring response rates throughout the intervals. While these different classes of procedures are supposedly equivalent in measuring temporal behavior, they have been found to produce divergent results (for a review, see Matthews & Meck, 2014). Our novel task measures both ongoing motion patterns and final choice at the end of the interval, which can be directly compared within each experiment and subject, but within each trial.

Fourth, learning about behavior during the sample has major implications for behavioral models that are largely based on the serial organization of behavior in time. Idiosyncratic behaviors during timing tasks are not always observed and the topographies of other behaviors do not necessarily correlate perfectly to the intervals (Shettleworth, 2010). Continuous motion, on the other hand, can easily correlate to time (Machado & Keen, 2003).

Finally, using this type of procedure may enrich some research topics in interval timing. For example, although it has shown to be interchangeable with the typical bisection task, this variation has a requirement of "filling time" with behavior (e.g., Harper & Bizo,

2000) that involves more physical effort (Molet, Alessandri, & Zentall, 2011) and thus could affect temporally-controlled behavior in new unforeseen ways. Additionally, it may bring insight into behavioral effects such as those presented in Figure 2 (panels B to D) – discrimination, bias and sensitivity –, and ultimately help clarify puzzling phenomena such as temporal distortions.

Temporal Bias

The properties of interval timing (Church, 2002b) may lead to the impression that timing is rigid and absolute. And, although researchers have noted that this is not necessarily the case since William James (1890), only towards the late 20th century has interest renewed in studying how timing can be flexible and relative (e.g., Maia & Machado, 2009; Morgan, Killeen, & Fetterman, 1993; Raslear, 1985). Anecdotal experience suggests that our perception of time is modulated by changes in the environment. It is not uncommon to hear the expression "Time flies when you are having fun!" or, conversely, "Time drags when you are bored".

Droit-Volet and Gil (2009) call this the *time-emotion paradox*: "Although humans are able to accurately estimate time as if they possess a specific mechanism that allows them to measure time (i.e. an internal clock), their representations of time are easily distorted by the context" (p. 1943). In other words, the way in which stimulus durations are perceived is distorted by, or dependent on, the context in which a task is conducted. Other references to similar phenomena are "temporal distortions" (e.g., Lake, LaBar, & Meck, 2016; van Wassenhove, Buonomano, Shimojo, & Shams, 2008), "illusions" (e.g., Eagleman, 2008; Matthews & Meck, 2014), or "biases" (e.g., Allan, 2002).

Most often than not, these modulations are referred to as over- or under-estimation of time (Molet et al., 2011) and attributed to a speeding-up or slowing-down of an internal clock mechanism (e.g., Simen & Matell, 2016). However, reporting results only in these terms makes it difficult to compare studies. Let's look at an example from Bindra and Waksberg (1956): In a task where an experimenter presents 15 s and obtains an estimation of 20 s, we could say that the participant overestimated the interval, and because less seconds had elapsed than the participant though, the subjective time was smaller than the objective time and thus the internal clock was faster. Alternatively, in a task where the experimenter presents 15 s and the participant reproduces 20 s, the participant also overestimated the interval, but one could say that the clock was *slower* because the subjective time units had to be larger to produce a 20 s count when the participant though it had produced 15 s.

The idea of distortions in temporal judgments may encompass changes in discrimination, bias, or sensitivity to temporal events, individually or in combination (e.g., Avlar et al., 2015). However, despite the vagueness and eventual contradiction in many of these explanations, the concept of temporal distortions tends to coincide with the quantitative measure of horizontal shifts in psychometric functions, i.e., a temporal biasing effect (Figure 2C; e.g., Stubbs, 1976), which will be the focus of this dissertation.

Evidence of biasing has been found in a variety of tasks with manipulations of the 1) Overall or general context, such as pre-experimental feeding (e.g., Roberts, 1981) and induced emotional states (e.g., Droit-volet, Brunot, & Niedenthal, 2004); 2) Sample stimulus, such as sensory modality (e.g., Droit-Volet, Tourret, & Wearden, 2004) and short—long ratio (e.g., Stubbs, 1968; J. H. Wearden & Ferrara, 1995; J. H. Wearden, Rogers, & Thomas, 2010); 3) Response requirements, such as number of pecks per reinforcer delivery (e.g., Zentall, Friedrich, & Clement, 2006; Zentall & Singer, 2008); and 4) Consequences for responding, such as the magnitude of reinforcers (e.g., Daniels, Fox, Kyonka, & Sanabria, 2015; Galtress & Kirkpatrick, 2009).

However, whether and how these and other non-temporal factors affect timing is still a poorly understood question. Many of these results are yet to be replicated. Further research is necessary because results are not always consistent between tasks or species (for a short review, see Matthews & Meck, 2014). Finally, it is still unclear whether some manipulations, usually comprised in the same category, are in fact equivalent. For instance, changes in the magnitude of reinforcers and pre-feeding are often referred to as "motivational variables" (e.g., Avlar et al., 2015; Galtress, Marshall, & Kirkpatrick, 2012), but one refers to amount of food per correct response while the other alters the overall value of food in a session.

Payoffs and Base-rates

Base-rate and payoff manipulations have been studied most comprehensively in a Signal Detection Theory approach to perceptual judgements (D. M. Green & Swets, 1966). While base-rate refers to the probabilities of presentation of stimuli, payoff refers to the probabilities of reinforcement. Interest in these variables arose from the study of categorization of continuous stimuli, especially when they differ in prevalence or costs and benefits (e.g., Healy & Kubovy, 1978; Kubovy & Healy, 1977; Lee, 1963; Lee & Janke, 1964; Lee & Zentall, 1966). Since response variability in categorization indicates perceptual noise, these manipulations were soon absorbed by a framework of optimal decision making, which focuses on the processes involved in base-rate and payoff learning (e.g., Bohil &

Maddox, 2001; Maddox, 2002; Maddox & Bohil, 1995, 1998b). Stimuli in the environment occur intermittently most often than not, thus the importance of understanding how we use this information to make decisions.

However, few studies have examined whether and how temporally-controlled responding is affected by these manipulations. This investigation is especially relevant in choice tasks such as the temporal bisection because responding “short” or “long” at the end of the sample involves decision making. One compelling question is the extent in which timing is sensitive to this probabilistic information derived from experience. In other words, if manipulating base-rate and payoff biases temporally-controlled responding, how large are the shifts in the PSE?

As a discrete-trials procedure, the temporal bisection task is the ideal setting to study temporal responding under differential base-rates for short and long samples because one of the intervals can easily be made more prevalent than the other. For example, one study by Jozefowiez, Polack, Machado, and Miller (2014) manipulated the frequency of short and long with human subjects and found results that agree with predictions of a modest bias. To our knowledge, these results were replicated once with humans (Çoşkun, Sayalı, Gürbüz, & Balcı, 2015) and with mice (Akdoğan & Balcı, 2016a).

Base-rate has been explored surprisingly little in interval timing experiments, even though many accounts of timing are strongly based on associative learning (e.g., BEM and LeT). The association between the presentation of stimuli of different durations and responding can be as important as the association between responses and their consequences. Base-rates may even be considered functionally similar to reinforcement contingencies (i.e., payoffs) in determining choice behavior (Catania, 1966; Nevin, 1969).

It is not surprising, however, that many more timing studies are interested in the effects of reinforcers. While an elementary procedure such as presenting response-contingent food periodically does not require discrimination between different stimulus durations, if an animal is sufficiently motivated, that is, deprived, it will do so. As well as the literature on time-markers, studies have observed that pre-feeding (e.g., Maricq, Roberts, & Church, 1981; Ward & Odum, 2007) and decreasing the overall rate of reinforcers (Bizo & White, 1994b, 1994a) produce rightward shifts in psychometric functions (a bias for long intervals). Intermittent reinforcers have been most explored in studies investigating effects of varying relative reinforcer rates (variable interval, VI, schedules of reinforcement) for the first and second half of trials (e.g., VI 45 *vs*. VI 90) in a free-operant psychophysical procedure.

Richer schedules on the first half shifted psychometric functions rightward, and on the second half, leftward (e.g., Bizo & White, 1995).

But manipulations of reinforcers are complicated in a bisection task because the need for a separate training and test phase means the overall probabilities of reinforcement are affected: introducing test durations (thus non-reinforceable) necessarily decreases payoffs in a session. To our knowledge, two attempts have been made to study the effect of differential reinforcement for "short" and "long" responses in a temporal bisection task. Stubbs (1976) manipulated reinforcer probabilities using a variation of the bisection task in which pigeons learned to choose one key following a range of short samples and another following long samples. The psychometric functions shifted in the direction of the richer key (bias) but sensitivity was not affected.

Galtress and Kirkpatrick (2010) exposed rats to a manipulation of reinforcer magnitudes (i.e., 1 *vs.* 4 pellets) using a standard bisection task. There was no consistent bias, but there was a loss in sensitivity when the number of pellets increased for correct "long" responses. The difficulty to interpret and extend these results to general timing principles alone warrants further investigation.

Timing Models

A series of quantitative models have been proposed to account for timing and uncover its underlying mechanisms. I will briefly discuss two predominant models in current psychology: The Scalar Expectancy Theory (SET) and the Learning-to-Time (LeT) model. I will compare how their predictions fare regarding a bias effect (shifts in response functions) of variables such as payoff and base-rate on timing processes and provide some support from the literature.

Scalar Expectancy Theory

The Scalar Expectancy Theory (SET; Church & Gibbon, 1982; Gibbon, 1977, 1991; Gibbon, Church, & Meck, 1984) is currently more of a class of cognitive models, rather than a single model. However, they all postulate that temporal information is processed by an internal clock with three main components: (a) a clock (pacemaker-accumulator), (b) memory, and (c) a comparator (Figure 3). The clock's pacemaker generates continuous pulses at a variable rate, which accumulate as a stimulus interval elapses. The number of pulses at a relevant time marker, such as the time of reinforcement, is stored in the reference, or long-term, memory. Tasks such as the temporal bisection, which involve learning at least two intervals, will form a different memory representation for each interval. When it is time to respond, the subject compares the current count of pulses in the accumulator (A) to one number randomly extracted from each memory (M_S and M_L), using a ratio threshold. If $A/M_S < M_L/A$, then the value in the accumulator is closer to the "short" memory and the subject responds accordingly. Else, if $A/M_S > M_L/A$, the response is "long". Finally, when $A/M_S = M_L/A$, the subject should be indifferent between the keys – the PSE. The straightforward way to test a SET-like model would be to see whether data from specific manipulations can be fitted from changes in any of the components of the model (J. H. Wearden & Grindrod, 2003).

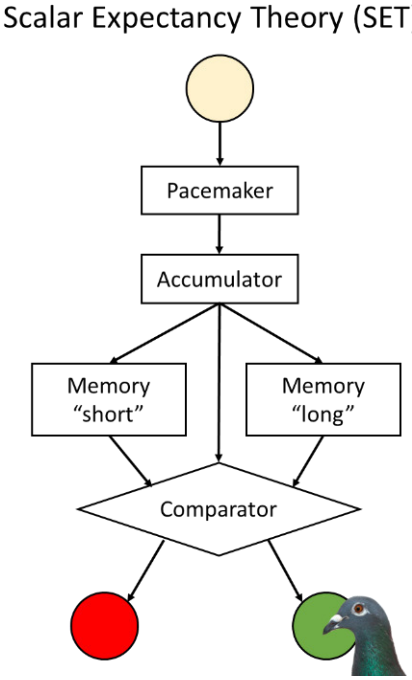

Figure 3. General structure of a Scalar Expectancy Theory model for a temporal bisection task. Yellow circle represents sample stimulus; red and green circles are pecking keys.

Memory. The memory component has received little to no attention in the temporal distortion literature. This is because although time of reinforcement is important for memory storage, the memory does not compute things such as rate or magnitude of the reinforcers, and thus could not explain any behavioral changes from payoff manipulations. Differential base-rates for short and long samples also would not affect responding because although each memory will have a different number of values, only one value will be selected from each memory and input to the comparator.

Clock speed. Changes in the average clock speed produce shifted functions, which could account for manipulations of reinforcers that are constant within trials, such as overall differences in reinforcement, prefeeding, and drug injection (e.g., Body et al., 2006; Buhusi & Meck, 2002; Galtress & Kirkpatrick, 2009; Meck, 1996; Morgan et al., 1993). However, this account is not able to predict *differential* effects of reinforcement on timing. The rate of the clock is retrieved from a random variable at trial onset and does not change as time elapses. With procedures like the bisection task, there is no discriminative stimulus at trial onset indicating which interval is active, nor the reinforcement rate/magnitude related to it.

Threshold. If the threshold in the SET comparator were to be affected by relative reinforcement, this would be represented in terms of shifts in response functions towards the choice producing higher payoff. Wearden and Grindrod (2003), for instance, used a "modified Church and Gibbon" model (MCG; J. H. Wearden, 1992) that allowed increasing reward magnitude to produce behavioral changes (more "yes" responses) consistent with an increase in the mean parameter of the response threshold. Smaller changes were also found in the standard deviation of the distribution in the memory component, which psychologically would be related to a "fuzziness" (p. 49) in temporal memory, although this is theoretically more difficult to interpret. However, a simulation by Jeremie et al (2014), with base-rates affecting the threshold, expressed almost absolute preference for the biased response, even though no experiments have shown such extreme biases, to the best of our knowledge.

Learning-to-Time

This is an associative model (LeT; Machado, 1997b) derived from the Behavioral Theory of Timing (BeT; Killeen & Fetterman, 1988), which also has three main components: (a) a set of behavioral states, (b) a set of associative links, and (c) operant responses (Figure 4). In its latest version (Machado et al., 2009), behavioral states are serially activated at a given rate (variable between trials), with the first behavioral state active at stimulus onset. Associative links connect states to responses and have initially the same strength. When the subject is reinforced for a response, the link between that response and the current behavioral state is strengthened (and the links of that response to the other states weakened), according to a reinforcement rule. When a response is not reinforced, the associative link between that response and the current state is weakened, according to an extinction rule. Thus, as training progresses, subjects have a higher probability of responding at the time of the active state with the greatest strength linked to that response.

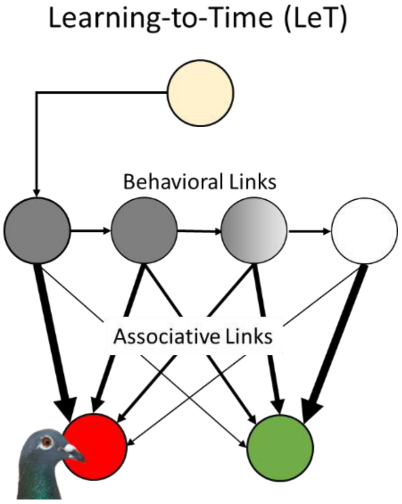

Figure 4. General structure of Learning-to-Time model for a temporal bisection task. Yellow circle represents sample stimulus; red and green circles are pecking keys.

LeT can account for shifts in response functions in a more straightforward way. Because associative links are affected by extinction (as well as reinforcement), connections become stronger between behavioral states and responses when reinforcement rate increases for that specific response. Machado and Guilhardi (2000) found evidence for this approach by showing that when reinforcement rate increases or decreases in the middle of a trial, not at the ends, response rate functions shift. On the other hand, SET's threshold account is a global and time-independent effect and would therefore predict shifts for relative rates independently of when the differential occurs. According to LeT, base-rate would also affect responding because each occurrence of a sample reinforces its corresponding response, so that by the end of training one response is more strengthened than the other.

Overall, these models make similar predictions for a series of different tasks and manipulations mainly because they were initially designed to account for the same set of timing phenomena (Church, 2002b). However, accounting for temporal distortion effects of non-temporal variables has been a more challenging endeavor considering the different types of manipulations described previously, and their somewhat heterogeneous effects on responding (mostly biasing, but sometimes loss in sensitivity or discrimination).

Further investigations must be conducted in order to establish precisely how different types of non-temporal manipulations affect timing (if at all). Looking at the model predictions can help us establish which phenomena they are able to account for and provide clues to new variations of models or even developing completely new timing models.

Models that can account for the results of these manipulations may help us better understand the relationship between timing and probabilistic information from differential base-rates and payoffs. For SET, timing and reinforcement are dissociable if changes affect the comparator, but not if they affect the internal clock; for LeT, any effects are inherently time-dependent, since reinforcement links sequential states to responding.

A Comparative Psychology of Timing

In a general sense comparative psychology studies similarities and differences in the behavior of organisms. Influenced by Thorndike's basic findings on learning through rewards, Skinner (1938; Ferster & Skinner, 1957) proposed general principles of learning that could be extrapolated across species. His groundbreaking research led to the definition of operant conditioning as behavior modified by its consequences, and of other general processes such as stimulus generalization (Wasserman, 1993, 1997).

However, using a large variety of procedures and species to study basic learning and perceptual processes means that exceptions to principles can always be found. One major issue in comparative psychology is the explanation for these differences. An obvious difference is physiological, for instance, pigeons are visual animals and naturally interact with the environment by pecking, while rodents have limited visual abilities and will rely mostly on hearing and manipulate objects with their paws. For that reason, operant chambers for pigeons will contain keys and those for rodents have levers.

Because of these differences, it is a challenging venture to make meaningful comparisons of the performance between species (Staddon & Cerutti, 2003). Are differences really between species or between tasks? For example, it is generally accepted that non-human animals are more impulsive than humans (Green & Myerson, 2004). Yet, while most human experiments involve hypothetical questions ("Would you rather have 1 dollar now or 5 dollars in a week?") and conditioned reinforcers, such as money (Johnson & Bickel, 2002; Kahneman & Tversky, 1979), animal experiments involve immediate food consumption, which is a primary reinforcer (e.g., Mazur, 2000). But providing humans with immediate consumable rewards has been shown to produce similar delay discounting curves as other animals (Estle, Green, Myerson, & Holt, 2007; Jimura, Myerson, Hilgard, Braver, & Green, 2009).

Nevertheless, even when tasks may be considered analogous, substantial differences may be found in the learning of two species. For instance, Bitterman (1965) found a qualitative difference in serial reversal: while rats' performance increased before declining, fish showed no improvement, only a tendency toward deterioration with extensive training. In a series of systematic procedural variations, performance did not change and could not be attributed to motor, sensory or motivational factors. Bitterman (1960, 1965) proposed to compare species in terms of their functional relations, that is, whether performance is affected "in the same way by the same variables".

This anagenetic approach (Greenberg, 1995) classifies species based on their common adaptive abilities regardless of phylogenetic relationship. Species can be defined in neurophysiological terms as well as behavioral processes that have a specific functional significance. The focus is not on quantitative comparisons across species, but on how the effects of functionally equivalent manipulations differ. Thus, when effects are similar across species, a related mechanism may be inferred. The "properties of timing" (Church, 2002b) may be considered one such attempt to find similarities between species, and timing models a pursuit for their underlying timing mechanisms.

Human and Non-human Studies in Interval Timing

Psychology is mainly interested in human processes and uses animal models to further this understanding. Thus, it is common in many areas of research to develop techniques for animal subjects based on previous studies on human behavior, or on behavioral phenomena observed in daily life. Examples range from learned helplessness as an animal model for some symptoms of depression (Seligman, 1972), to pigeons gambling in a slot machine (Fortes, Case, & Zentall, 2017).

In interval timing, few papers have directly addressed the issue of a comparative psychology (for a review, see Lejeune, 1993). One important question is the degree to which the principles and mechanisms of timing in non-human animals are like those found in humans. Fetterman and Killeen (1992) for instance, directly compared time discrimination of pigeons and humans, producing similar results: the data were well described by the generalized form of Weber's law (Getty, 1975). More recently, Daniels, Fox, et al. (2015) compared the temporal performance of rats, pigeons, and humans, and observed significant differences, especially regarding human data *versus* rats and pigeons. An analogous task and experimental manipulation (increasing the magnitude of reinforcement in a switch task) produced decreases in the standard deviation of the response latency function of rats and humans, but not pigeons. The mean parameter decreased for rats and pigeons, but unexpectedly increased for humans.

Most currently used procedures in timing originated from animal experiments and analogous techniques were developed to test and compare human performance. Some examples include the temporal generalization procedure (Church & Gibbon, 1982), the peak procedure (Catania, 1970), and the temporal bisection task (Church & Deluty, 1977; Platt & Davis, 1983) transposed to computer tasks with human subjects (Rakitin et al., 1998; Wearden, 1992; and Wearden, 1991, respectively).

One controversial discovery is the location of the point of subjective equality (PSE), since non-human animals bisect intervals at the geometric mean (c.f. Raslear, 1983), while humans were initially found to bisect at the arithmetic mean (J. H. Wearden, 1991). However, finding the PSE at the geometric mean for humans (Allan & Gibbon, 1991) suggested that the behavior of all animal species could be explainable using the same model. The explanation for this discrepancy in the literature may lie in parametric differences in the task, such as spacing between the short and long durations (e.g., J. H. Wearden & Ferrara, 1995).

One important phylogenetic difference between humans and other species is verbal behavior. Human performance is often rule-governed as opposed to contingency-shaped. Participants will often follow self-generated rules and ignore the experimental contingencies, especially when instructions are inaccurate (Baumann, Abreu-Rodrigues, & da Souza, 2017; Galizio, 1979). Avoiding self-produced interpretations has led to animal-like performance in fixed-interval schedules (Bentall, Lowe, & Beasty, 1985; Lowe, Beasty, & Bentall, 1983), and is thus one way to improve comparability between species.

In timing, counting strategies may mediate temporal judgements (e.g., Rakitin et al., 1998). Thus, there may be advantages in preventing this behavior by instructing participants to avoid counting or rhythmic activities (Rattat & Droit-Volet, 2012), or by using very short durations that frustrate attempts at counting (Fetterman & Killeen, 1991). However, participants may ignore instructions and report counting (Daniels, Fox, et al., 2015). Even without reports of counting there may be differences with other species (Wearden & Lejeune, 1993).

Finally, it is also questionable whether psychology students receiving college credits for their participation are motivated to offer their best performance during experiments. Perception tasks are often prolonged and strenuous, and extended exposure to repetitive stimuli often leads to reports of tediousness and decrease in attention. “Gamification,” or designing nongame activities to be more like a game, has become increasingly popular first in applied settings for teaching socially significant behaviors, and more recently in basic research (for a review, see Morford, Witts, Killingsworth, & Alavosius, 2014). For example, Guilhardi, Menez, Caetano and Church (2010) used a version of the peak procedure consisting of a bulls-eye target that moved across the screen for participants to shoot at, reproducing scalar timing results in a more entertaining setting.

The Present Dissertation

Considering a need to increase our comprehension of basic interval timing processes under a behavioral perspective, the main goal of the present dissertation is to investigate the effects of manipulating two key contextual variables – payoff and base-rate – on the temporally controlled performance of human and non-human animals as assessed by a bisection task.

To accomplish this goal, we established a series of specific objectives:

a) Evaluate the effects of these non-temporal variables on bias, sensitivity, and discrimination measures of temporal discrimination;
b) Emphasize effects at an individual level by adopting a within-subject design;
c) Employ the "novel" bisection task to obtain further behavioral measures of timing;
d) Relate and contrast the effects of differential base-rates and payoffs;
e) Compare performance between species, namely *Columbia livia* and *Homo sapiens*;
f) Consider the implications of our results for timing models.

In Chapter II, we start by investigating the effects of payoffs on pigeons. Although reinforcers are the more explored environmental variable, biasing is not a robust finding for the standard temporal bisection task. We propose a series of arrangements to deal with the training-test issue. We also used a custom-built long operant chamber with sensitive floor panels, similar to the one used by Machado and Keen (2003), to record motion patterns during the sample and compare parameters to the psychometric function. In our preparation, the birds are initially trained to step on the panels closest to the pecking keys to turn on their respective hues, to avoid signal-tracking (i.e., running towards the lit key that appears first in their field of vision).

In Chapter III, we replicate the previous study with a base-rate manipulation. This underrepresented variable still warrants further investigation with different species, parameters, and preparations. We tested the generality of the effect with pigeons in the long operant chamber. Unlike previous studies, reinforcers were delivered intermittently for correct responses. Programming equal overall reinforcement rates in both studies' baselines accomplishes a more plausible comparison between base-rate and payoff effects and makes way for future studies integrating both variables.

In Chapters IV and V, we created an analogous task for humans and manipulated payoff and base-rate, respectively. In the standard temporal bisection task, participants learned a discrimination between very short intervals and go through three biasing conditions in one session. We used auditory stimuli so the onset of the stimuli would not be missed (we can look away and shut our eyes, but not our ears). We then conceived an adaptation of the "novel" bisection task from the operant chamber to a computer game. Two aliens, equal in size, shape and color were placed at each side of the screen, with a spaceship at the center. During the sample (a sound), participants could displace the spaceship horizontally, but pressing to shoot had no effect. At sample offset, the "shoot" key was enabled, and pressing it would kill the alien immediately above. We established a limited hold, so that motion during the sample was negatively reinforced by avoiding being shot by the aliens and terminating the trial.

Finally, in Chapter VI we summarize and relate the large volume of data from the experiments, draw conclusions, and make suggestions for this rich sub-field of interval timing. The comparison between pigeons and humans aims to encourage analysis of possible differences and why they occur. If they are procedural, then we will have learned something to advance our methods. Integrating this information should help further develop models of timing and ultimately our understanding of the basic processes of interval timing across species.

CHAPTER II [1]

DIFFERENTIAL PAYOFF EFFECTS ON PIGEONS

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[1] This Chapter reproduces the publication:

Cambraia, R., Vasconcelos, M., Jozefowiez, J. & Machado, A. (2019). Biasing performance through differential payoff in a temporal bisection task. *Journal of Experimental Psychology: Animal Learning and Cognition*. DOI: 10.1037/xan/0000192

I would like to thank Catarina Vila Pouca for collecting data for Experiment 1 and Nicole Sobral Félix for help collecting data for Experiment 2.

Abstract

We investigated how differential payoffs affect temporal discrimination. In a temporal bisection task, pigeons learned to choose one key after a short sample and another key after a long sample. When presented with a range of intermediate samples they produced a Gaussian psychometric function characterized by a location (bias) parameter and a scale (sensitivity) parameter. When one key yielded more reinforcers than the other, the location parameter changed, with the pigeons biasing their choices toward the richer key. We then reproduced the bisection task in a long operant chamber, with choice keys far apart, and tracked the pigeons' motion patterns during the sample. These patterns were highly stereotypical – on the long sample trials, the pigeons approached the short key at sample onset, stayed there for a while, and then departed to the long key. The distribution of departure times also was biased when the payoff probabilities differed. Moreover, it is likely that temporal control decreased while control by location increased. No evidence was found of changes in temporal sensitivity. The results are consistent with models of timing that take into account bias effects and competition of stimulus control.

Reinforcement affects temporal discrimination in multiple ways. Reducing the overall probability of reinforcement, for example, may change sensitivity to the time dimension and induce response biases (e.g., Bizo & White, 1994a, 1994b; Galtress & Kirkpatrick, 2009; Killeen & Fetterman, 1988; Morgan, Killeen & Fetterman, 1993). However, the effects of differential reinforcement remain unclear. Few studies have investigated the issue and those that have did not yield consistent results. As Matthews and Meck (2014) noted, the effects of different variables on temporal discrimination may depend on seemingly minor procedural details that vary across tasks.

Consider the Free-Operant Psychophysical Procedure (FOPP; Stubbs, 1980). Two manipulanda, such as a left and a right key for pigeons, are available for the duration of a trial. During the first half of the trial, only choices of the left key are reinforceable, whereas during the second half only choices of the right key are reinforceable. Two independent Variable Interval (VI) schedules set up the reinforcers for each choice during the corresponding trial half.

The typical finding is that the proportion of responses to the right key increases with time into the trial. This psychometric function has a sigmoidal shape, ranging from approximately 0 at trial onset to approximately 1 at trial offset. Two of its properties are especially relevant to characterize performance. First, the moment the function crosses the indifference line. This is the function's *location* parameter, usually called the Point of Subjective Equality or PSE, and measures bias. Second, the slope of the function at indifference. This is the *scale* parameter, and measures sensitivity to stimulus durations (Gibbon, 1981).

Bizo and White (1995) varied the reinforcement rates in the two trial halves of a FOPP and found that pigeons biased their choices toward the key associated with the richer schedule. Specifically, when the VIs were equal, the PSE revealed no bias; when the VIs favored the right key (e.g., VI 120 s for left, VI 40 s for right), the pigeons shifted to the right key earlier than in the baseline and the PSE was shorter; when the VIs favored the left key (e.g., VI 40 s for left, VI 120 s for right), the pigeons shifted to the right key later than in the baseline and the PSE was longer. These findings were later extended by Machado and Guilhardi (2000) with pigeons, and by Guilhardi, MacInnis, Church, and Machado (2007) with rats. None of these studies found any effects of the payoff differential on sensitivity.

Cowie, Bizo, and White (2016) also used a FOPP with pigeons to examine the effects on bias and sensitivity of both overall payoff (the average of the two VIs) and relative payoff (the difference or ratio of the two VIs). They found that changes in overall reinforcement rate did not seem to affect sensitivity or bias; yet, in contrast with Machado and Guilhardi (2000) and Guilhardi et al. (2007), Cowie and colleagues found greater sensitivity and response bias when the second half of the trial was richer than the first half.

Unlike the FOPP, in a temporal bisection task, responses are made only after a to-be-timed stimulus has elapsed: On each trial a sample stimulus (e.g., a houselight) is presented for either a short (S) or a long (L) duration, and then the subject chooses between two comparisons, say, a left lever and a right lever; one choice is rewarded following S and the other choice is rewarded following L. After the animal learns the two sample-comparison mappings, the experimenter introduces test samples with intermediate durations and records the proportion of "long" choices (i.e., choices of the lever rewarded following L) after each sample. The resulting psychometric function is also sigmoidal; it increases with time from approximately 0 to approximately 1 and has a PSE close to the geometric mean of the two trained samples (Church & Deluty, 1977).

To study the effect of differential payoff in a bisection task, Galtress and Kirkpatrick (2010) exposed rats to the discrimination S = 2 s and L = 8 s. In baseline, all correct choices were reinforced with one food pellet. Next, one group of rats received a fourfold increase in reward magnitude for correct responses to L, whereas another group received the same increase for correct responses to S. Compared to baseline, the psychometric functions obtained with different reinforcement magnitudes for S and L flattened (loss in sensitivity) but did not shift (bias) consistently. That is, when the payoff differential stemmed from differences in reward magnitude, biasing was not a robust finding as in the FOPP experiments.

Stubbs (1976) used a variation of the bisection task to study the effect of payoff probability on temporal discrimination. Pigeons learned to choose a red key following short samples (from 11 to 15 s) and a green key following long samples (from 16 to 22 s). The payoff probabilities for correct choices were manipulated according to a complex rule – each correct choice had two effects, it illuminated the magazine light, and it counted toward the completion of a Variable Ratio (VR) 4 schedule requirement. When the number of correct choices equaled the current VR requirement, one reinforcer was allocated, with probability p to the red or "short" key, and with probability 1-p to the green or "long" key. The reinforcer remained allocated until collected. Across conditions, Stubbs varied p from 0 to 0.875. The psychometric functions shifted in the direction of the richer key – a biasing effect –, but sensitivity remained approximately constant.

Stubbs' (1976) results are difficult to interpret and extend to the standard, two-sample bisection task. First, any generalization effects due to the differential payoff following the shortest and longest samples were masked by the strengthening effects of the reinforcers following the intermediate samples. Second, the reinforcement rule (withholding a reinforcer until collected) forced the pigeons to maintain some responding to the least-reinforced key, which may have prevented the expression of more extreme biases. In fact, when p=0 (no reinforcers followed red key pecks), all three pigeons continued to choose the red key on at least 30% of the trials. This surprising result – for one would expect extinction of responses to the red key when choices of red ceased to be reinforced – may have been due to a long history with a schedule that (when $p \neq 0$) eventually reinforced the least-preferred choice. Third, other procedural features (e.g., no ITI, use of magazine light as a conditioned reinforcer), absent from the typical bisection task, may further limit the generality of Stubbs' findings.

In the present study, we revisit the standard temporal bisection task to examine how different probabilities of reinforcement for short and long responses affect the psychometric function. Let p and q be the reinforcement probabilities given correct choice following the Short and Long samples, respectively, and let Δ be the payoff differential (i.e., $\Delta = p{-}q$). Note that Δ depends exclusively on the payoff probabilities associated with the two training samples. Across phases, we varied Δ and checked its effects on the psychometric function.

To obtain the psychometric function, the experimenter must present new sample durations during generalization tests. But how should these tests be conducted to isolate the effects of Δ? Specifically, should the tests eliminate the differences in reinforcement probability used in training (i.e., train with $\Delta \neq 0$, but always test with $\Delta = 0$), or should the tests maintain the training Δ? Because both options seem sensible, we adopted the first strategy in Experiment 1A and the second strategy in Experiment 1B.

Thus, in Experiment 1A we varied the Δ across conditions, from -0.9 to $+0.9$, and then, after each condition, we obtained a psychometric function with $\Delta = 0$. To illustrate, in one condition we reinforced 10% of the correct "Short" choices ($p = 0.1$) and 100% of the correct "Long" choices ($q = 1.0$), for a $\Delta = p{-}q = -0.9$; after training, we tested with a range of sample durations, including the S and L trained durations. Choices following the new samples were never reinforced, but correct choices following S and L were equally reinforced with $p = q = 1$ ($\Delta = 0$).

In contrast, in Experiment 1B, the just described training condition was followed by test sessions in which the p and q values remained unchanged ($\Delta = -0.9$ in training and testing), but in this case, to maintain the overall probability of reinforcement approximately constant, the new sample durations were nondifferentially reinforced. By using different testing procedures, we expected to find converging evidence concerning the effects of differential reinforcement on temporal discrimination.

In Experiment 2, we examined the effect of Δ on temporal discrimination using a different apparatus, one that afforded additional measures of temporal discrimination. Pigeons performed the bisection task in a long operant chamber with the choice keys far apart and sensitive floor panels (Machado & Keen, 2003). In addition to choice responses, the chamber allowed us to track the pigeon's location during the trial. By studying the pigeon's motion patterns, particularly during the sample, we expected to better understand how the payoff differential affects temporal discrimination.

To illustrate, suppose the left key is always correct following the S sample, and the right key is always correct following the L sample. In this "time-place learning task" (Wilkie & Willson, 1992; Wilkie, Saksida, Samson, & Lee, 1994), pigeons typically display a stereotypical motion pattern during the L samples – they move to the *short* (left) side at sample onset, stay on that side past the duration of the S sample, and then depart to the *long* (right) side. Their stereotypical motion pattern, correlated with the sample duration, externalizes the putative internal clock and its study may help us understand the effects of Δ. Thus, when Δ differs from 0, does the pigeon move to the *long* side earlier or later than usual? Does it move at sample onset to the wrong, i.e., *long* side of the box? Does it move back and forth at times close to the geometric mean of S and L? Moreover, the parameters of the motion patterns (e.g., mean time to leave the *short* side on Long samples) may yield behavioral measures more sensitive to reinforcement variables than choice proportion.

To summarize, across two experiments, using different testing strategies and apparatus, we ask whether pigeons respond more to the alternative associated with a higher payoff probability (a bias effect revealed by a shift in the psychometric function), and whether they also show changes in sensitivity to stimulus duration (revealed by changes in the slope of the psychometric function). Additionally, we investigate behavior during the sample and how it relates to final choice. Overall, this set of experiments will contribute to resolve conflicting claims in the literature and help us better understand the effects of differential reinforcement on temporal discrimination.

Experiment 1A

In Experiment 1A, we varied Δ during the training conditions with the S and L samples, but always tested with the same Δ = 0 after each condition; moreover, untrained samples were never reinforced. We reasoned that, if learning during test trials is relatively slow, testing under the same conditions better isolates the effects of training under different Δs. However, because learning is likely to take place during testing, prolonged exposure to the test conditions would eventually eliminate the effects induced during training. Therefore, we limited testing to two sessions after each condition.

Method

Subjects. Six pigeons (*Columba livia*) maintained at 80% of their free-feeding weights participated in the experiment. All subjects had previous experience with choice procedures, including timing tasks. Water and grit were continuously available in their individual home cages. The pigeons were housed in a colony room with controlled temperature (between 20º and 22º C) and a 13:11h light:dark schedule with lights on at 8:00 A.M. All the animals were cared for according to the guidelines from the Portuguese Veterinary Agency (Direcção Geral de Alimentação e Veterinária).

Apparatus. Four identical Lehigh Valley® operant chambers for pigeons were used. Each chamber was 34 cm x 35 cm x 31 cm (height x length x width). The walls and ceiling were made of aluminum and the floor was a wire mesh. Centered on the back wall of the chamber, 4 cm below the ceiling, a 28-V, 0.1-A houselight provided general illumination. The response panel contained three circular keys, 2.5 cm in diameter, arranged in a horizontal row, 22.5 cm above the floor and 9 cm apart, center to center. Reinforcement consisted of mixed grain delivered by a hopper that was accessible through a 6 cm x 5 cm opening, centered horizontally on the response panel, 8.5 cm above the floor. A 28-V, 0.04-A white light illuminated the opening whenever a reinforcer was available. An outer box equipped with a fan for ventilation (and to help mask outside noises) enclosed the experimental chamber. A personal computer equipped with Whisker software (Cardinal & Aitken, 2010) and running a custom written Microsoft Visual Basic 2008 program controlled all experimental events and recorded the data with a temporal resolution of 1 ms.

Procedure. In pre-training, pigeons were required to peck at the side keys under a multiple Fixed-Ratio (FR) 5 schedule. Each schedule was in effect randomly and occurred equally often. This lasted for five sessions and all subjects obtained at least 90% of the programmed reinforcers by the last session. In all other phases, they were exposed to a temporal bisection task. All trials followed the same general structure: After a 20-s dark inter-trial interval (ITI), the houselight and the center key (white hue) illuminated simultaneously. During training, the sample could last either 3 s (Short) or 9 s (Long). After the sample elapsed, the houselight and the white center key turned off and the side keys turned on, each with a different hue, red or green. A single peck at one of the illuminated side keys turned them off and, if the choice was correct, it gave the pigeon access to grain. The duration of access to grain varied across birds from 3 to 5 s. It was adjusted for each bird during the first sessions to minimize extra-session feeding. After the reinforcer, the ITI followed. If the choice was incorrect, the ITI followed immediately. Correct, non-reinforced trials, were also immediately followed by the ITI.

The position of the green and red key colors varied randomly across trials with the constraint that, at the end of each session, each color had appeared equally often in each position. For three pigeons (P190, P639, P785), choosing the green key after Short samples and the red key after Long samples were considered correct responses; for the other three (P284, P588, P841) the reverse assignment was in effect. For generality, we will refer to the trained Short (S) and Long (L) samples together as anchors and to the corresponding choices as “short” and “long”.

Discrimination Training. Initially, all trials were baited, that is, all trials were reinforced provided the choice was correct. Incorrect responses repeated the trial (correction procedure). In the first session, a single error led to a forced trial in which only the correct comparison key was illuminated after the sample. In the second session, forced trials occurred after two consecutive errors. From the third session onward, the pigeon had to make three consecutive errors to start a forced trial. Sessions comprised 60 randomly intermixed trials (30 S, 30 L), excluding correction trials (see Table 1, row 1). Training continued for a minimum of 15 sessions and until the birds met the learning criterion of 70% correct choices per sample for five consecutive sessions.

Next, we added extinction trials to reduce the proportion of baited trials, first to .75 and then to .5. Consider the second row of Table 1 (Discrimination Training): At the beginning of each session the computer selected 30 of the 40 trials of each type (S and L) randomly and baited them. If the pigeon made a correct choice on those trials, it received food; on the remainder 10 non-baited trials, the pigeon did not receive food, even if it chose correctly. When the proportion of baited trials equaled .5, we removed the correction procedure for the remainder of the experiment. When the birds met the learning criterion of 70% correct choices per sample for five consecutive sessions, they advanced to the test phase.

Generalization Test. This phase consisted of two sessions with 96 trials each; 48 were baited trials with the anchor durations (24 S, 24 L), and 48 were unreinforced trials with three new sample durations (3.95, 5.20, and 6.84 s, each presented 16 times). Together with the 3.0 s and 9.0 s anchors, these durations form a geometric series with an approximate ratio of 1.32; the 5.20 s duration corresponds to the geometric mean of the two training samples.

Table 1

Proportion of Baited Trials per Trial Type (Short, Long, or Probes) and Corresponding Payoffs for Experiment 1A During Training and Test Phases

Condition	Phase	Baited trials/Total			Payoff				
		Short	Long	Probes	*p*	*q*	Δ	Probes	Overall
	Discrimination Training	30/30	30/30	-	1.00	1.00	.00	-	1.00
		30/40	30/40	-	.75	.75	.00	-	.75
		24/48	24/48	-	.50	.50	.00	-	.50
	Generalization Test	24/24	24/24	0/48	1.00	1.00	.00	.00	.50
LB$_{(0.1-1.0)}$	Training	6/60	60/60	-	.10	1.00	-.90	-	.55
	Test	24/24	24/24	0/48	1.00	1.00	.00	.00	.50
LB$_{(0.1-0.5)}$	Training	6/60	30/60	-	.10	.50	-.40	-	.30
	Test	24/24	24/24	0/48	1.00	1.00	.00	.00	.50
NB$_{(0.5-0.5)}$	Training	30/60	30/60	-	.50	.50	.00	-	.50
	Test	24/24	24/24	0/48	1.00	1.00	.00	.00	.50
SB$_{(0.5-0.1)}$	Training	30/60	6/60	-	.50	.10	+.40	-	.30
	Test	24/24	24/24	0/48	1.00	1.00	.00	.00	.50
SB$_{(1.0-0.1)}$	Training	60/60	6/60	-	1.00	.10	+.90	-	.55
	Test	24/24	24/24	0/48	1.00	1.00	.00	.00	.50

Note. LB = long bias; NB = no bias; SB = short bias.

Payoff Training. Experimental conditions differed only in the payoff probabilities for S and L, p and q. These payoffs were manipulated across five conditions (see Table 1), favoring the “short” response (Short Bias, SB), the “long” response (Long Bias, LB), or none (No Bias, NB). For example, in condition $LB_{(0.1\text{-}1.0)}$, only 10% of the S trials were baited whereas 100% of the L trials were baited. Conversely, in condition $SB_{(1.0\text{-}0.1)}$, 100% of the S trials were baited whereas only 10% of the L trials were baited. Sessions comprised 120 trials, 60 with each sample. After 5 sessions, the test phase began.

Payoff Test. The Payoff Test phase lasted for two sessions, and these were exactly equal to the Generalization Test phase sessions.

The pigeons went through the five conditions shown in Table 1 according to a Latin square design with one repeat (P190 and P841 ran in the same order, starting with $LB_{(0.1\text{-}1.0)}$).

Results and Discussion

All subjects learned the bisection task during Discrimination Training. When 100% of the trials were baited, they required on the average (range) 16.5 (15 – 20) sessions to meet the learning criterion; when only 50% of the trials were baited, they required 6.2 (5 – 9) additional sessions to meet the criterion. At the end of training, the proportion of correct responses averaged .93 (.84 – .98) for S and .87 (.83 – .93) for L. A paired-sample t-test showed that the performance was slightly better at short samples, $t(5) = 2.74$, $p = .02$, $d = 1.27$.

Figure 5 shows the average psychometric function (symbols) from the Generalization Test. As expected, the proportion of “long” responses increased smoothly as a function of sample duration; choice following the trained samples remained accurate (cf. filled and empty circles at 3- and 9-s samples). The curve through the data points shows the average of the individual best-fitting functions.

To characterize the individual psychometric functions, we fitted each of them with a two-parameter Gaussian distribution function by the method of least-squares. The best-fitting location parameter, μ, estimates the PSE. The best-fitting scale parameter, σ, is inversely proportional to the slope of the function at the PSE, with larger values (flatter functions) indicating lower sensitivity to sample duration. Table A1 in Appendix A lists the best-fitting parameters and R^2.

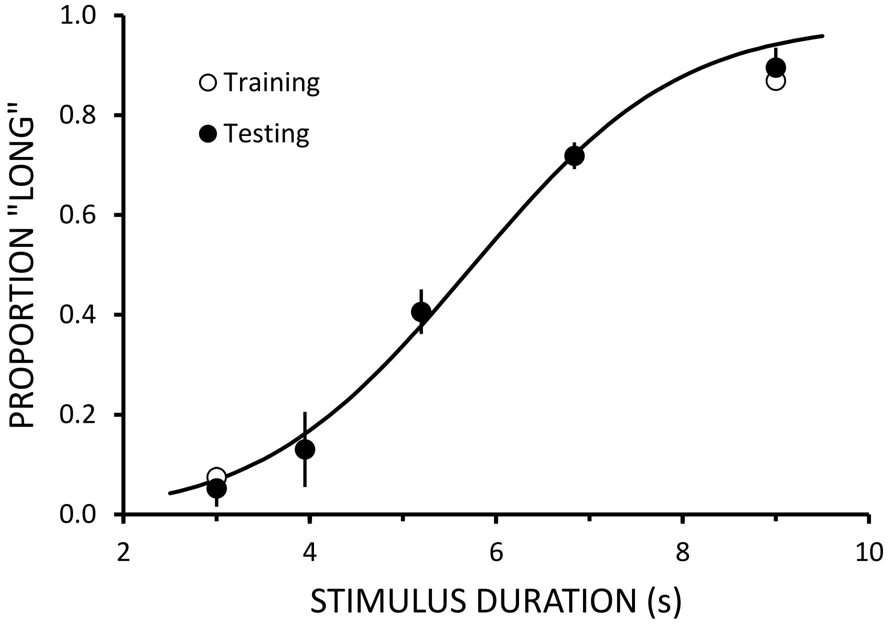

Figure 5. Proportion of "long" responses (M ± SEM) as a function of stimulus duration obtained in the Generalization Test (filled circles) and curve with averaged parameters from individually fitted cumulative Gaussians (solid line) in Experiment 1A. Unfilled circles show the average proportion of "long" responses for the last five sessions of Discrimination Training.

The average fitted function (see Figure 5) accounted well for the average of the observed functions ($R^2 = .98$). The location parameter, or PSE, averaged 5.83 s (*SEM* = ±0.31), a value greater than the geometric mean (5.2 s) but less than the arithmetic mean (6 s) of the trained durations. The scale parameters averaged 1.84 (*SEM* = ±0.31). These results are typical of the bisection task with non-human animals (e.g., Catania, 1970; Church & Deluty, 1977; Fetterman & Killeen, 1991; Killeen & Fetterman, 1988; Machado, 1997; Morgan, Killeen, & Fetterman, 1993; Platt & Davis, 1983; Stubbs, 1968).

To assess the biasing effect of Δ, Figure 6 shows the average psychometric function obtained in each condition during the first (top panel) and second (bottom panel) Payoff Test sessions. In Test 1, when the payoff favored the "long" response, the functions shifted to the left, whereas when the payoff favored the "short" response the functions shifted to the right. A repeated-measures ANOVA, with Condition and Duration as factors, confirmed a significant main effect of condition, $F(4, 20) = 10.722$, $p < .001$, $\eta_p^2 = .682$ and signal duration, $F(4, 20) = 2.393$, $p < .001$, $\eta_p^2 = .962$, and a significant interaction, $F(16, 80) = 2.029$, $p = 0.021$, $\eta_p^2 = .289$.

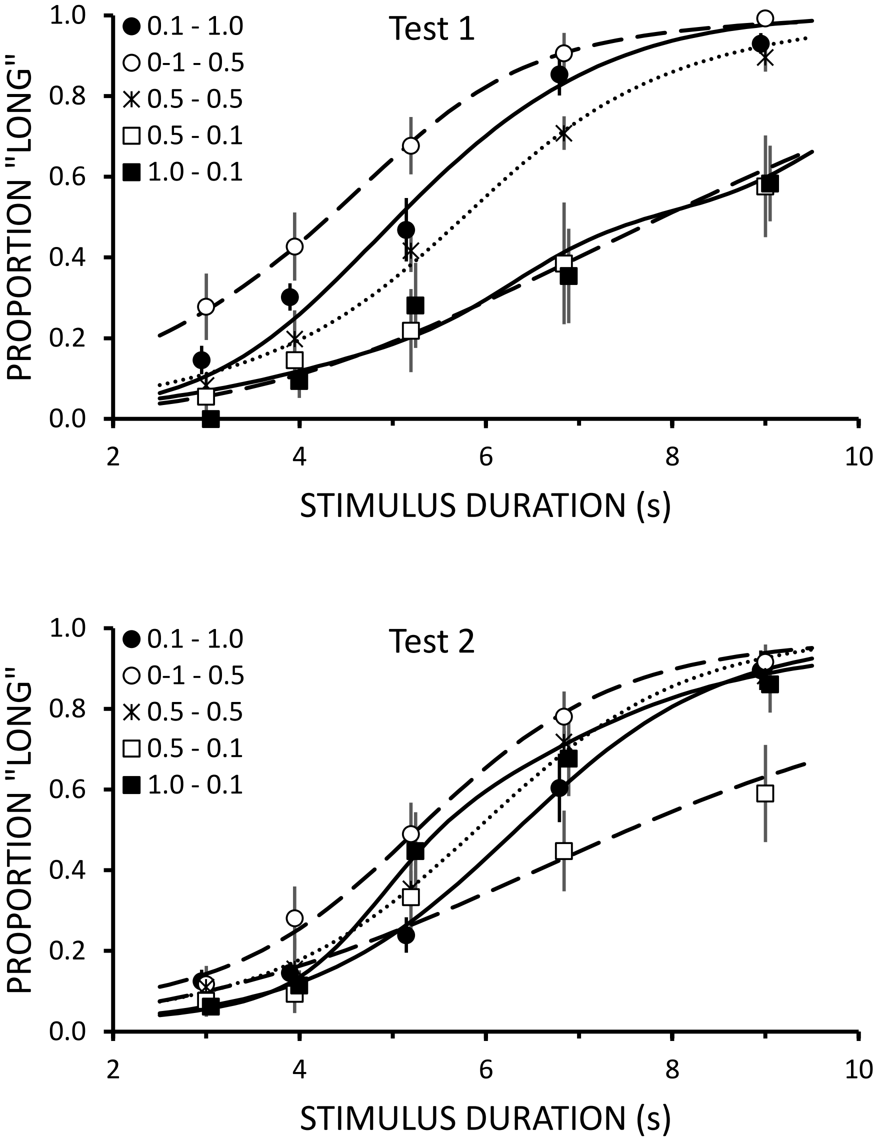

Figure 6. Proportion of "long" responses (M ± SEM) for each condition: $LB_{(0.1\text{-}1.0)}$ (filled circles), $LB_{(0.1\text{-}0.5)}$ (empty circles), $NB_{(0.5\text{-}0.5)}$ (asterisks), $SB_{(0.5\text{-}0.1)}$ (empty squares) and $SB_{(1.0\text{-}0.1)}$ (filled squares), and corresponding curves with averaged parameters from individually fitted cumulative Gaussians (solid lines for $\Delta = \pm 0.9$, dotted lines for $\Delta = \pm 0.4$, dashed line for $\Delta = 0$), in Experiment 1A. Top and bottom panels show the first and second test sessions, respectively.

Although the pigeons never lost the discrimination between the anchors, accuracy decreased following the sample associated with the lower payoff (cf. circles at 3 s and squares at 9 s). The effect was noticeable following the long sample in the SB conditions (rightmost squares). Cowie et al. (2016), also found a lower maximum when the first half of the trial had a higher reinforcement rate even though FOPP experiments have not typically found significant changes in maximum response rates.

It is noteworthy, however, that the two conditions with the greatest payoff differential, conditions $LB_{(0.1\text{-}1.0)}$ with $\Delta = -0.9$ and $SB_{(1.0\text{-}0.1)}$ with $\Delta = +0.9$, did not yield stronger biases than conditions $LB_{(0.1\text{-}0.5)}$ and $SB_{(0.5\text{-}0.1)}$ ($\Delta = \pm0.4$). This result differs from Bizo and White (1995), the only other study to compare a range of Δ values, who found that larger payoff differentials yielded greater shifts of the psychometric function.

Test 2 yielded similar results concerning stimulus durations, $F(4, 20) = 191.082$, $p < .001$, $\eta_p^2 = .975$, but smaller differences among conditions, $F(4, 20) = 3.506$, $p = .025$, $\eta_p^2 = .412$. The five psychometric functions overlapped more in Test 2 than in Test 1 which means that bias decreased across test sessions. Because the biasing effect was stronger in Test 1, we restrict subsequent analyses to the first test session.

Figure 7 shows the average location (μ; top) and scale (σ; bottom) parameters from the individually fitted cumulative Gaussian distribution functions for Test 1. The dotted horizontal lines indicate the average values from the Generalization Test. Visual inspection of individual parameters (Appendix A) revealed that P190 in condition $SB_{(0.5\text{-}0.1)}$, had very large values compared to the other conditions and pigeons. The empty circles indicate the average with the outlier excluded.

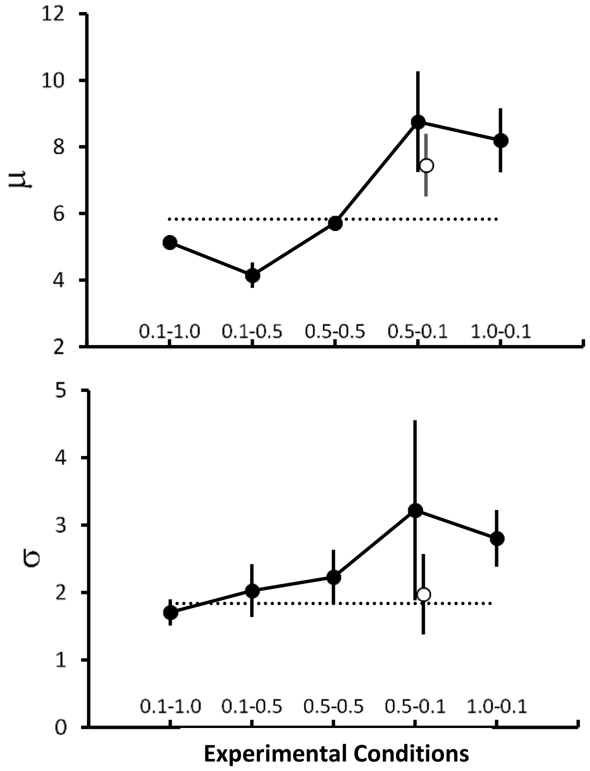

Figure 7. Average parameters per condition from individual cumulative Gaussian fits: μ (top), σ (bottom) of Experiment 1A. Open circles indicate values excluding an outlier. Dotted horizontal lines indicate values from the Generalization Test.

A repeated measures ANOVA conducted with all subjects indicated that the location parameters differed significantly across conditions, $F(4, 20) = 5.859$, $p = .003$, $\eta_p^2 = .540$, showing the expected trend, LB < NB < SB, and the scale parameters did not differ across conditions, $F(4, 20) = 0.751$, $p = .569$, $\eta_p^2 = .131$. In short, bias varied with Δ, although not monotonically, but sensitivity to stimulus duration did not.

Why didn't bias vary monotonically, as in previous experiments (Bizo & White, 1995; Stubbs, 1976)? The effect on response bias may have been due to the changes in the overall proportion of baited trials (*O*) from training to testing, with larger differences yielding stronger biases. Thus, because the changes in *O* from training to testing were largest in conditions $\text{LB}_{(0.1\text{-}0.5)}$ and $\text{SB}_{(0.5\text{-}0.1)}$, intermediate in conditions $\text{LB}_{(0.1\text{-}1.0)}$ and $\text{SB}_{(1.0\text{-}0.1)}$, and smallest in condition $\text{NB}_{(0.5\text{-}0.5)}$, the magnitude of the response bias was similarly ordered. Previous studies have found similar effects when manipulating overall rates of reinforcement, i.e., the higher the rate, the greater the shift (Bizo & White, 1994a, 1994b). We examine this interpretation in Experiment 1B.

Experiment 1B

In Experiment 1A, training with different Δs and testing with the same Δ meant that testing conditions were equal throughout the experiment. However, it also meant that the payoffs associated with the trained samples changed by different amounts in the transition from training to testing. We do not know whether these different amounts of change obscured the effects of training with different Δs. Experiment 1B addresses this issue because the Δ used during training remained in effect during testing. By non-differentially reinforcing the intermediate durations, *O* remained approximately equal in training and testing within a condition. If the results remain as in Experiment 1A, we can rule out the hypothesis that changes in bias stem from changes in *O* from training to testing. In this case, we will also have found converging evidence that Δ affects bias regardless of testing conditions.

Method

Subjects and Apparatus. The same six pigeons from Experiment 1A participated in this experiment. Housing conditions and apparatus remained as in Experiment 1A.

Procedure. ***Payoff Training.*** The payoff conditions (Table 2) were the same as those of Experiment 1A, with trials and sessions following the same structure. Order of conditions for each bird also remained the same. To ensure more stable psychometric functions in each condition, the criterion to advance to the test phase was stable performance for three consecutive sessions, with a minimum of five and maximum of ten sessions per condition.

Table 2

Proportion of Baited trials per Trial Type (Short, Long, or Probes) and Corresponding Payoffs for Experiment 1B During Training and Test Phases

Condition	Phase	Baited trials/Total			Payoff				
		Short	Long	Probes	p	q	Δ	Probes	O
$\text{LB}_{(0.1\text{-}1.0)}$	Training	6/60	60/60	-	.10	1.00	-.90	-	.55
	Test	4/40	40/40	16/32	.10	1.00	-.90	.50	.54
$\text{LB}_{(0.1\text{-}0.5)}$	Training	6/60	30/60	-	.10	.50	-.40	-	.30
	Test	4/40	20/40	8/32	.10	.50	-.40	.25	.29
$\text{NB}_{(0.5\text{-}0.5)}$	Training	30/60	30/60	-	.50	.50	.00	-	.50
	Test	20/40	20/40	16/32	.50	.50	.00	.50	.50
$\text{SB}_{(0.5\text{-}0.1)}$	Training	30/60	6/60	-	.50	.10	+.40	-	.30
	Test	20/40	4/40	8/32	.50	.10	+.40	.25	.29
$\text{SB}_{(1.0\text{-}0.1)}$	Training	60/60	6/60	-	1.00	.10	+.90	-	.55
	Test	40/40	4/40	16/32	1.00	.10	+.90	.50	.54

Note. LB = long bias; NB = no bias; SB = short bias.

Payoff Test. The payoff differential, Δ, remained the same in training and testing. To maintain overall proportion reinforced, O, also approximately constant from training to testing, the probe samples were partially reinforced regardless of choice (for details, see Table 2). We also introduced two new probe durations (1.73 s and 15.6 s) to check biasing effects on samples outside the range of the trained samples. Test sessions comprised 112 trials each, including 80 anchors (40 S, 40 L) and 32 probes. There were two types of sessions. Type 1 sessions included samples of 1.73 s, 5.20 s, and 15.6 s, each presented for 8, 16, and 8 trials, respectively. Type 2 sessions included samples of 3.95 s and 6.84 s, each presented for 16 trials. After two test sessions (in random order), there was one session of Payoff Training with the same Δ for the current experimental condition. Testing ended after 4 test sessions.

Transition. Because testing now maintained the Δ from training, the experimental conditions were separated by a transition phase to reduce potential carry-over effects. Transition consisted of a minimum of three training sessions equal to the No-Bias condition, NB$_{(0.5\text{-}0.5)}$. To advance, birds had to maintain a stable performance, with no visible trend in choice proportion over the last three sessions.

Results and Discussion

Figure 8 shows the average psychometric functions obtained in the Payoff Test phase of each condition and the corresponding curves obtained from the averaged best-fitting individual Gaussian functions (Table A2 in Appendix A lists the best-fitting parameters). Overall, as the signal duration increased, a strong preference for "short" transitioned smoothly to an almost absolute preference for "long". As in Experiment 1A, accuracy at the anchors decreased when the payoffs favored the opposite response (cf. circles at 3 s and squares at 9 s). However, adding durations outside the trained range shows that samples longer than L had almost exclusively "long" responses, and samples shorter than S had almost exclusively "short" responses. A repeated-measures ANOVA with Condition and Duration as within-subject factors, yielded significant main effects of condition, $F(4, 20) = 15.443$, $p < .001$, $\eta_p^2 = .755$, sample duration, $F(6, 30) = 304.380$, $p < .001$, $\eta_p^2 = .984$, and their interaction, $F(24, 120) = 4.505$, $p < .001$, $\eta_p^2 = .474$.

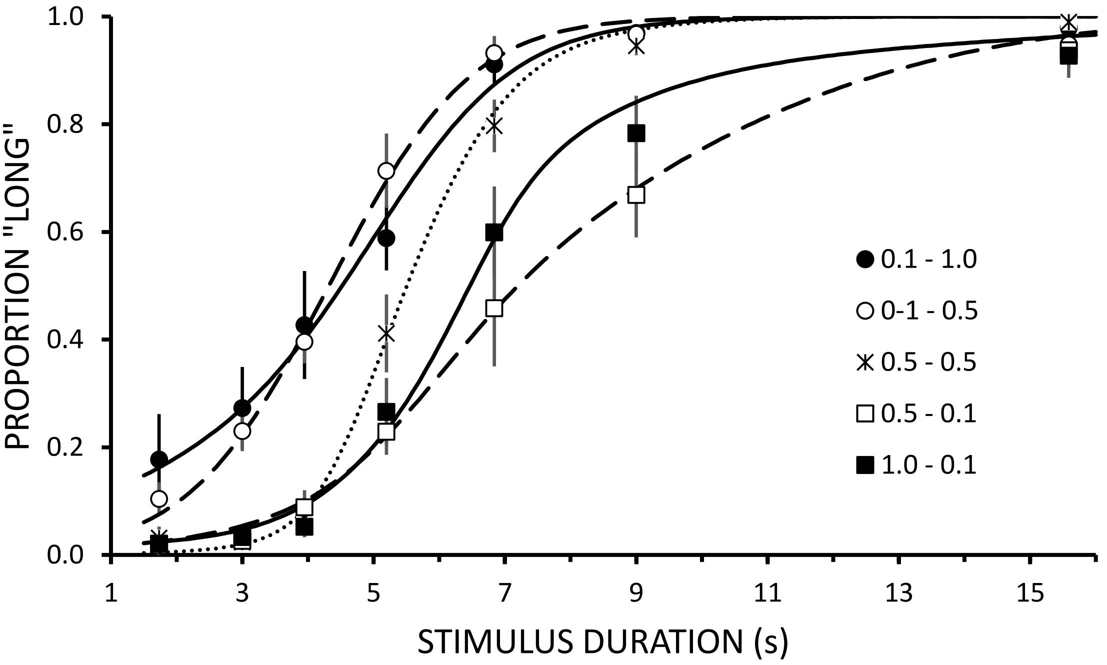

Figure 8. Proportion of "long" responses (M ± SEM) for each condition: LB$_{(0.1\text{-}1.0)}$ (filled circles), LB$_{(0.1\text{-}0.5)}$ (empty circles), NB$_{(0.5\text{-}0.5)}$ (asterisks), SB$_{(0.5\text{-}0.1)}$ (empty squares) and SB$_{(1.0\text{-}0.1)}$ (filled squares), and corresponding curves with averaged parameters from individually fitted cumulative Gaussians (solid lines for $\Delta = \pm 0.9$, dotted lines for $\Delta = \pm 0.4$, dashed line for $\Delta = 0$), in Experiment 1B.

Thus, when the reinforcement contingencies favored the “long” response, the psychometric functions shifted to the left, whereas when they favored the “short” response the functions shifted to the right (Figure 8). The location parameters from the individual Gaussian fits corroborated this finding. As the top panel of Figure 9 shows, the PSE varied with Δ: It was smaller in conditions with higher payoff for “long” and larger in conditions with higher payoff for “short”. A repeated measures ANOVA yielded significant differences in μ across conditions, $F(4, 20) = 9.352$, $p < .001$, $\eta_p^2 = .652$.

Although the averaged psychometric functions in Figure 8 suggest a difference in slope, there was substantial variability in choice proportion at the durations around the PSE. The scale parameters from the Gaussian fits, displayed in the bottom panel of Figure 9, revealed no clear changes in sensitivity with Δ, $F(4, 20) = 1.927$, $p = .145$, $\eta_p^2 = .278$. To summarize, as in Experiment 1A, the effect of differential payoff was expressed as horizontal shifts in the psychometric functions and the consequent change in PSE, but not as changes in sensitivity.

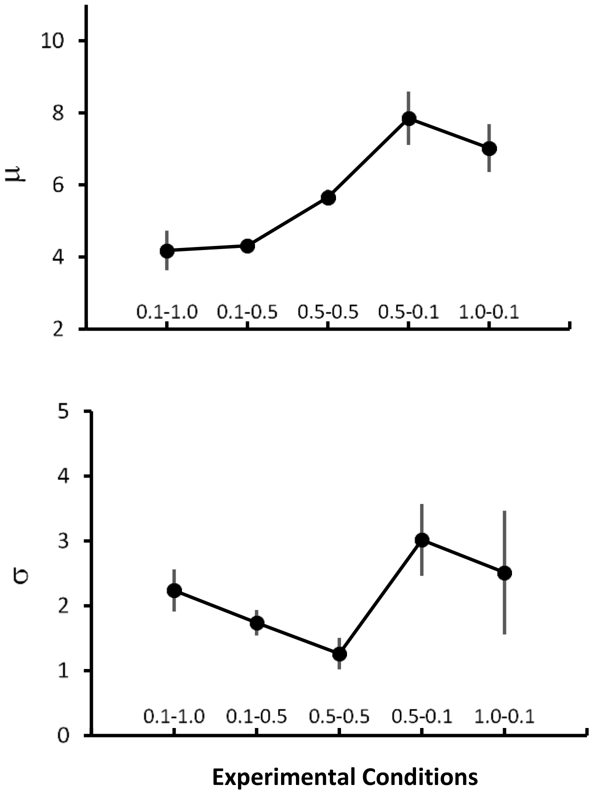

Figure 9. Average parameters per condition from individual cumulative Gaussian fits: μ (top), σ (bottom) of Experiment 1B.

Experiments 1A and 1B extended to the standard bisection task the payoff manipulation investigated in previous studies (Bizo & White, 1995; Cowie et al., 2016; Daniels, Fox, Kyonka, & Sanabria, 2015; Guilhardi et al., 2007; Stubbs, 1976). Our results showed that higher payoffs change response bias, but not sensitivity to time. Although the two studies differed in several procedural aspects, in both the direction of the shifts of the psychometric functions covaried with the sign of Δ, whereas the magnitude of the shifts seemed to depend non-monotonically on the absolute value of Δ.

The non-monotonic effects of Δ on bias suggest that the effect of Δ may be modulated by differences in O between conditions, although exactly how remains unclear. One possibility is by a Weber-like ratio Δ/O, as suggested, e.g., by Machado, Keen, and Macaux (2008), and Machado and Keen (1999), with O possibly raised to a power (i.e., Δ/O^k). In fact, the PSE has a positive correlation with the simple ratio Δ/O in Experiment 1A ($M = 0.73$; range: 0.21 – 0.97) and Experiment 1B ($M = 0.85$; range: 0.72 – 0.94). Only future studies in which Δ and O are varied systematically and independently can shed further light on the functional form relating these two variables to response bias.

Experiment 2

In Experiment 2 we used a long operant chamber to observe behavior during the sample. With a similar apparatus, Machado and Keen (2003) reported that pigeons discriminated the trained samples and acquired a highly stereotypical motion pattern, a pattern fully displayed during the long-sample trials: At sample onset, the birds move to the side associated with S, wait a few seconds, and then depart to the side associated with L and stay there until the sample ends. The authors also showed that the moment of switching from the *short* to the *long* side (i.e., the departure time or DT) could be used as a trial-by-trial measure of the PSE. Mean DT may thus be considered as an alternative to the PSE obtained from a psychometric function. Moreover, the Empirical Cumulative Distribution Function of DT proved to be equivalent to the choice-based psychometric function in the sense that it predicted the proportion of "long" choices given a new sample duration.

Daniels, Fox, Kyonka, and Sanabria (2015) found evidence of reinforcement-induced biases in temporal discrimination by observing switching from a *short* to a *long* lever on a concurrent fixed-interval schedule (Conc FI 8 s FI 16 s). Specifically, they examined the effects of reward magnitude on the latency to switch from the short to the long FI in pigeons, rats, and humans. In non-human animals, increases in payoff for the long FI produced a bias for long, i.e., earlier switching. In addition, whereas sensitivity did not change with payoff in pigeons, it decreased with higher payoffs for "long" in rats.

Analyzing behavior during the interval may help us understand the timing processes taking place during the sample as well as how they relate to choice when reinforcement differs for "short" and "long" responses. This "hybrid" procedure obtains the typical measures from the temporal bisection task and approximates it to others that measure responding throughout the timed interval (i.e., the FOPP and the "switching" task). To simplify the experiment, we used only two Δ values, –0.6 and +0.6 and, as in Experiment 1B, these values remained in effect during testing. We also changed the test phases to better isolate the effects of Δ. First, we reduced the number of probe trials to maintain relatively similar overall reinforcement probabilities, *O*, from Training to Testing without having to reinforce non-differentially the new samples. More importantly, *O* also remained approximately constant across conditions. The experiment checked the generality of the findings obtained with the standard operant chamber.

Method

Subjects. Six pigeons maintained at 80% of their free-feeding body weights participated in the experiment. All had previous experience with standard operant chambers in experiments related to choice in concurrent chain schedules. Housing conditions remained as in Experiment 1.

Apparatus. Figure 10 shows a schematic of the long chamber. Overall dimensions were 96 x 31 x 33 cm (length x depth x height). The back and side walls were made of 3-mm thick aluminum panels, and each was equipped with one houselight (28 V, 0.1 A), horizontally centered and 1.5 cm from the ceiling; three circular response keys, 2.5 cm in diameter, 24 cm above the floor, and 8 cm apart, center-to-center; and one feeder opening, 6 cm wide x 5 cm high, horizontally centered, and 9 cm above the floor. A 28-V, 0.04-A light illuminated the grain when a feeder was activated. All other walls and the ceiling were made of acrylic. The pigeons were placed inside the chamber through the front wall, which was hinged to the floor.

The floor consisted of three rectangular aluminum panels, placed side by side, each with a fulcrum in the middle and two switches underneath, one at each end. The box was divided lengthwise into six segments, numbered 1 (leftmost) to 6 (rightmost). When the bird moved to one segment, the corresponding panel tilted and activated the switch at that location. Thus, the numbers 1–6 indicate the bird's location.

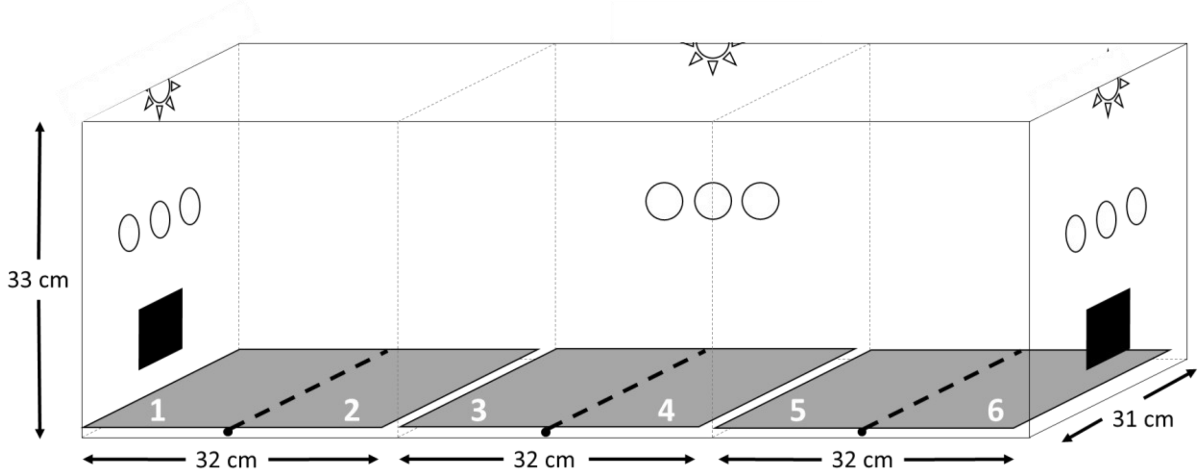

Figure 10. Schematics of the long operant chamber.

The chamber was placed on a shelf rack in a closed laboratory room, 10 cm from the floor, and isolated visually by a black curtain placed 10 cm in front of the chamber. A computer on the shelf above controlled all experimental events and recorded the data using ABET II® software (Lafayette Instruments). A webcam, placed 5 cm in front of the bottom left corner of the box, and connected to a laptop computer on the top shelf, allowed the experimenter to observe inside the chamber.

Procedure. Pigeons were initially trained to eat from all three feeders and to peck the left key of the left panel, the center key of the center panel and the right key of the right panel (hereafter referred to as left key, center key and right key). They were then trained across six sessions on the following two chains, a) peck the green center key, step on location 1 to turn on the red left key, peck the left key, and receive food from the left feeder; and b) peck the green center key, step on location 6 to turn on the red right key, peck the right key, and get food on the right feeder. This training ensured that the animals learned to illuminate and then peck a side key by standing on locations 1 and 6.

In all subsequent phases, pigeons performed a bisection task with S = 3 s and L = 12 s. The L sample was slightly longer than in Experiment 1 to better track displacement during the L samples. All trials followed the same general structure: After a 20-s ITI[1] with only the center houselight on, the center key was illuminated with green light. A single peck changed the key light to red and turned on both the left and right houselights. Thus, pigeons were at the center of the chamber at trial onset. After the sample elapsed, the center key and the side houselights turned off. The pigeon could then turn on with red light the left or right keys by stepping on locations 1 or 6, respectively. When it pecked an illuminated side key, it received food from the corresponding feeder provided the response was correct. For three subjects, the left key was correct on S trials and the right key was correct on L trials; for the other three, the opposite assignment was in effect. Sessions ended when the birds obtained all scheduled reinforcers.

Discrimination Training. To maintain the behavioral chains intact, on 10% randomly selected trials in each session, pecking at the green center key was reinforced immediately by raising the center feeder. These trials were not further analyzed. The remaining 80 trials (40 S, 40 L; see Table 3) were all baited, and a correction procedure was in effect. During the first session, a single error led to a forced trial, in which only the correct comparison key could be turned on after the sample. During the second session, forced trials occurred only after two consecutive errors. From the third session onward, three consecutive errors were necessary to start a forced trial.

Table 3

Proportion of Reinforced Trials per Trial Type (Short, Long, or Probes) and Corresponding Payoffs for Experiment 2 During Training and Test Phases

Condition	Phase	Reinforced trials/Total			Payoff				
		S	L	Probes	*p*	*q*	Δ	Probes	*O*
	Discrimination Training	40/40	40/40	-	1.00	1.00	.00	-	1.00
		30/40	30/40	-	.75	.75	.00	-	.75
		20/40	20/40	-	.50	.50	.00	-	.50
LB$_{(0.2-0.8)}$	Training	8/40	32/40	-	.20	.80	-.60	-	.50
	Test	8/40	32/40	0/16	.20	.80	-.60	.00	.41
NB$_{L(0.5-0.5)}$	Training	20/40	20/40	-	.10	.50	.00	-	.50
	Test	20/40	20/40	0/16	.10	.50	.00	.00	.41
SB$_{(0.8-0.2)}$	Training	32/40	8/40	-	.80	.20	+.60	-	.50
	Test	32/40	8/40	0/16	.80	.20	+.60	.00	.41
NB$_{S(0.5-0.5)}$	Training	20/40	20/40	-	.10	.50	.00	-	.50
	Test	20/40	20/40	0/16	.10	.50	.00	.00	.41

Note. LB = long bias; NB = no bias; SB = short bias.

The learning criterion was eight or fewer errors per sample, excluding correction trials. When the birds met the learning criterion for three consecutive sessions and had completed a minimum of 15 sessions, the proportion of baited trials decreased to .75. The correction procedure remained in effect on these trials, but not on the .25 extinction trials. This phase lasted until the learning criterion was met for five consecutive sessions.

Next, the proportion of baited trials was further reduced to .5. During the first sessions, feeder durations were adjusted individually to minimize extra-session feeding (final range: 1.5 – 2.1 s). For this and subsequent training phases of the experiment, the correction procedure remained in effect but the forced trials were eliminated. When the birds met the learning criterion for five consecutive sessions, they advanced to the first payoff manipulation phase.

Payoff Training. The bisection task remained the same across conditions except for the p and q values. Table 3 shows the details for each condition. In the No-Bias, $NB_{(0.5\text{-}0.5)}$ conditions, 50% of the trials for each sample were baited; in Long-Bias, $LB_{(0.2\text{-}0.8)}$, 80% of the L trials and 20% of S trials were baited. In Short-Bias, $SB_{(0.8\text{-}0.2)}$, 20% of the L trials and 80% of S trials were baited. For all conditions, the overall payoff, O, remained constant at .5.

Half of the subjects started with condition $SB_{(0.8\text{-}0.2)}$ (P463, P116, and P536) and the other half started with condition $LB_{(0.2\text{-}0.8)}$. To minimize carry-over effects, $NB_{(0.5\text{-}0.5)}$ conditions occurred after each biasing condition: $NB_{S(0.5\text{-}0.5)}$ and $NB_{L(0.5\text{-}0.5)}$ followed $SB_{(0.8\text{-}0.2)}$ and $LB_{(0.2\text{-}0.8)}$, respectively. Training phases of each condition were in effect for at least ten sessions. To advance to the test phase of each condition, the pigeons had to meet the learning criterion for at least three consecutive sessions.

Payoff Test. Test sessions followed each Training phase. They introduced non-reinforced probe trials with new sample durations. The S and L samples were reinforced with the same p and q values used during the preceding Training phase, but the correction procedure was not in effect. Besides the 80 anchor trials (40 S, 40 L), 18 probe trials were added with the sample durations of 1.5, 4.2, 6, 8.5, 17, and 24 s (three trials per duration). The shortest (1.5 s) and longest (24 s) test durations were half of S and double of L, respectively. Together with the training signals, the durations approximate a geometric series with ratio 1.4; 6 s is the geometric mean of the trained signals. Testing lasted 6 sessions.

Analysis of motion patterns. To analyze the motion patterns during the sample, we assume that, for all subjects, the *short* and *long* sides corresponded to locations 1 and 6, respectively. Let $\lambda(t)$ denote the pigeon's location at time t, with $\lambda(t) = 1, 2,\ldots,6$, and $0 \leq t \leq$

sample duration, with t measured in 0.5-s bins. We define Arrival Time at the *short* side (AT_S) as the time since sample onset at which $\lambda(t)$ reached its minimum value (i.e., the time it was closest to location 1). Thus, if a pigeon moved from the center to the *short* side such that $\lambda = 1$ for the first time at $t = 4.3$ s, then $AT_S = 4.3$ s. If the pigeon later moved to location 6, we defined the Departure Time to the *long* side (DT) as the time the pigeon first stepped on location 2, the location immediately higher in the direction of location 6. If, on another trial, location 2 was the closest to the *short* side the bird arrived at before moving to location 6 (i.e., if $\lambda(AT_S) = 2$), then DT equaled the time the pigeon first stepped on location 3 in its way to location 6. Finally, if the pigeon was in location 3, say, at sample onset, did not move for a while, and then moved to the long side, its $AT_S = 0$ and its DT would be the time it first reached location 4. As these examples show, we define a DT only on trials the pigeons moved to the *long* side. Residence time at the *short* side equaled DT- AT_S, and Arrival Time at the *long* side (AT_L) equaled the first moment $\lambda(t) = 6$.

Results and Discussion

Discrimination Training. Acquisition was similar across pigeons, who met the learning criterion after 4.3 sessions on average (range: 3 – 6). Figure 11 shows a representative example. In each panel, the solid line represents the median location at time t; the lower and upper dotted lines represent the first and third quartiles. The successive panels show the acquisition of the temporal discrimination, the learning to approach the *short* side, waiting there past the S duration, and then moving to the *long* side. The variability of the motion patterns decreased across sessions.

In the last session before we reduced the reinforcement probabilities, the pattern shown in the top right panel accounted for 96% (averaged across subjects) of all long trials. The pigeons arrived at the *short* side (AT_S) on average 2.53 s into the sample (*SD* = 0.81 s). They left the *short* side (DT) by 5.14 s (1.54 s) and arrived at the long *side* (AT_L) by 7.56 s (2.26 s), where they generally remained until the end of the trial. Thus, when all correct responses were reinforced, the birds' motion patterns became more stereotypical with training.

The bottom panels of Figure 11 show the motion patterns from the last sessions of the 75% (left) and 50% (right) reinforcement phases. Compared with the 100% condition, the changes were small and consisted mainly in a slight increase in the variability of the motion patterns. The acquisition patterns replicate Machado and Keen (2003).

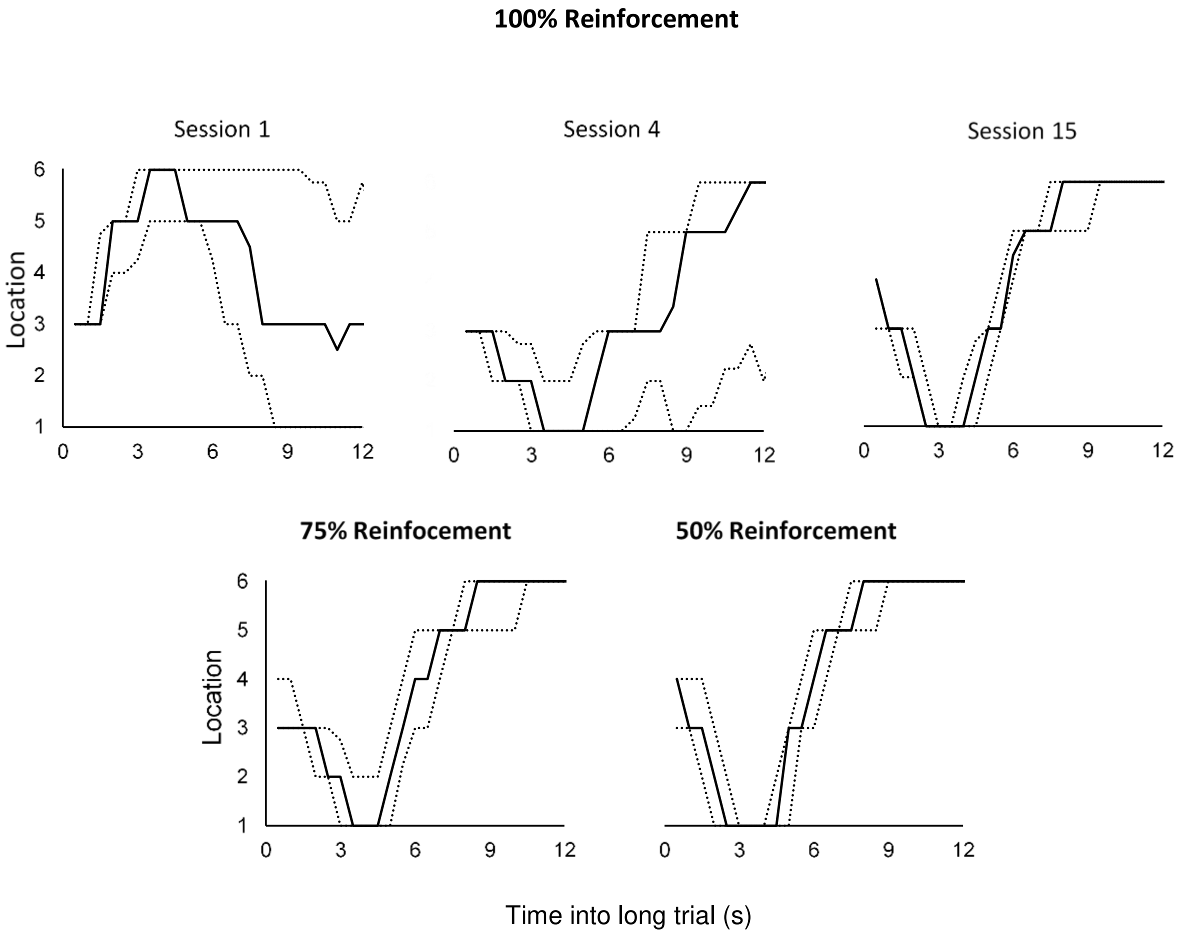

Figure 11. Motion patterns for bird P501 in Discrimination Training. Top panel: Acquisition patterns obtained with 100% reinforcement for both samples. The leftmost graph shows the first session, the middle graph shows an intermediate session (first session before learning criterion was met), and the rightmost graph shows the last session in this phase. Bottom panel: Left graph shows last session with 75% reinforcement; right graph shows the last session with 50%. The three lines are, from top to bottom, the third (dotted line), second (solid line), and first (dotted line) quartiles of the birds' location during the long trials. Training samples were 3- and 12-s long.

Proportion of "long" choices. The psychometric functions for each pigeon and condition, and their individually fitted Gaussian functions, are shown in Figure 12. Average functions and fits are presented in the bottom panel. Given the large range of stimulus durations and the fact that responding at and outside the anchors yielded almost exclusive preference, duration is plotted in a logarithmic scale (Table B1, in Appendix B, lists the best-fitting parameters).

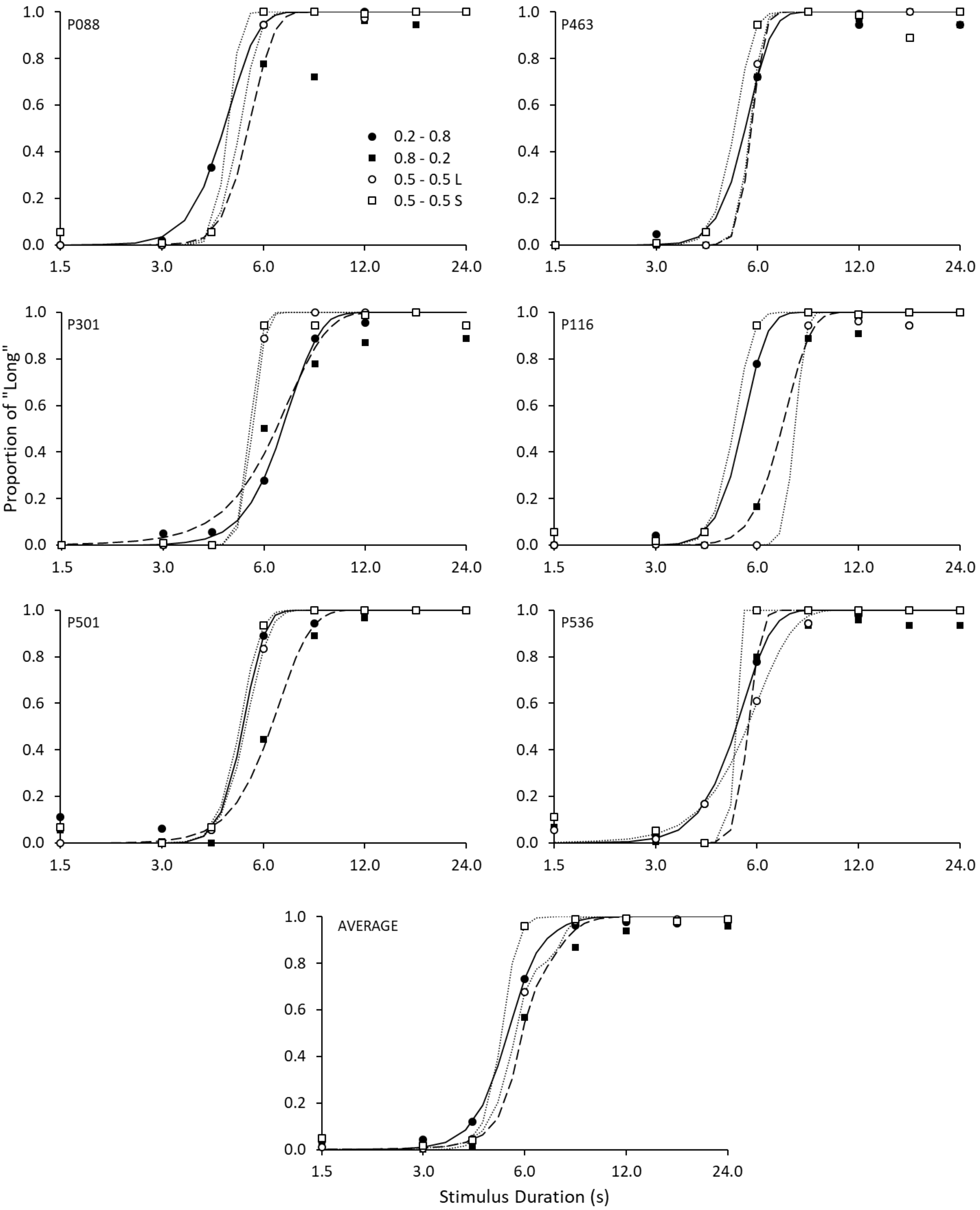

Figure 12. Proportion of "long" responses for each condition: LB$_{(0.2\text{-}0.8)}$ (solid circles), NB$_{L(0.5\text{-}0.5)}$ (empty circles), SB$_{(0.8\text{-}0.2)}$ (filled squares), NB$_{S(0.5\text{-}0.5)}$ (empty squares), and corresponding individually fitted cumulative Gaussians (solid lines LB$_{(0.2\text{-}0.8)}$ and SB$_{(0.8\text{-}0.2)}$, dotted lines for NB), in Experiment 2. The left panel shows pigeons that started on LB$_{(0.2\text{-}0.8)}$ and the right panel shows pigeons that started on SB$_{(0.8\text{-}0.2)}$. Bottom graph shows average data.

A repeated-measures ANOVA of the psychometric functions yielded significant effects of Condition, $F(3, 15) = 6.388$, $p = .005$, $\eta_p^2 = .561$, Duration, $F(7, 35) = 413.297$, $p < .001$, $\eta_p^2 = .988$, and their interaction $F(21, 105) = 2.937$, $p < .001$, $\eta_p^2 = .370$. The μ parameter from the fits also differed across conditions, $F(3, 15) = 3.986$, $p = .028$, $\eta_p^2 = .444$, but the σ parameter did not, $F(3, 15) = 2.432$, $p = .105$, $\eta_p^2 = .327$. These findings are consistent with the results from Experiment 1, that is, changing Δ affected response bias but not sensitivity.

Detailed analysis of the individual psychometric functions (Figure 12) shows that choice proportion during the $NB_{(0.5\text{-}0.5)}$ conditions tended to approach step functions, with responding close to or at 0 for durations below 6 s and responding close to or at 1 for durations at or longer than 6 s. Thus, PSEs were generally below 6 s ($M = 5.4$, $SEM = 0.22$) except for P116, with PSE = 7.76 s in $NB_{L(0.5\text{-}0.5)}$. Machado and Keen (2003) also found categorical-like responding with PSEs below the geometric mean when 100% of both samples were baited.

Unlike baseline, psychometric functions for unequal payoff show a smoother transition from 0 to 1. Thus, PSEs for $NB_{(0.5\text{-}0.5)}$ did not tend to fall between $LB_{(0.2\text{-}0.8)}$ and $SB_{(0.8\text{-}0.2)}$. Because LB and SB were our manipulations of interest, we conducted further analyses to compare them. The leftward shifts of $LB_{(0.2\text{-}0.8)}$ functions compared to $SB_{(0.8\text{-}0.2)}$ (except P301) were small, but the PSEs were significantly different (paired-sample $t(5) = 2.015$, $p = .031$ (one-tailed), $d = 0.985$). Despite significant variability across pigeons, these effects were in the same direction as found in the literature as well as Experiment 1.

Motion patterns. Because the motion patterns produced in the last three sessions of each payoff training phase were similar to those observed in the six test sessions that followed, the former are not shown. Figure 13 shows the individual motion patterns (median only) during long trials for all test sessions in conditions $LB_{(0.2\text{-}0.8)}$ and $SB_{(0.8\text{-}0.2)}$.

In general, the birds maintained the stereotypical pattern observed in training, going to the short side and remaining there for a few seconds, and then moving to the long side. Although there was no difference in arrival times (AT_S), departures for the long side (DT) were on average earlier in condition $LB_{(0.2\text{-}0.8)}$ ($M = 4.94$ s, $SD = 0.31$) than in condition $SB_{(0.8\text{-}0.2)}$ ($M = 5.66$ s, $SD = 0.37$), $t(5) = 6.533$, $p < .001$, $d = 2.07$. The shift entailed longer residence times in condition $SB_{(0.8\text{-}0.2)}$ ($M = 3.30$ s, $SD = 0.66$) than in condition $LB_{(0.2\text{-}0.8)}$ ($M = 2.64$ s, $SD = 0.55$), $t(5) = 9.765$, $p < .001$, $d = 1.08$. P536 shows an especially large difference between conditions, for it went directly to the long side on 52% of the L trials in condition $LB_{(0.2\text{-}0.8)}$, but only on 11% of those trials in condition $SB_{(0.8\text{-}0.2)}$.

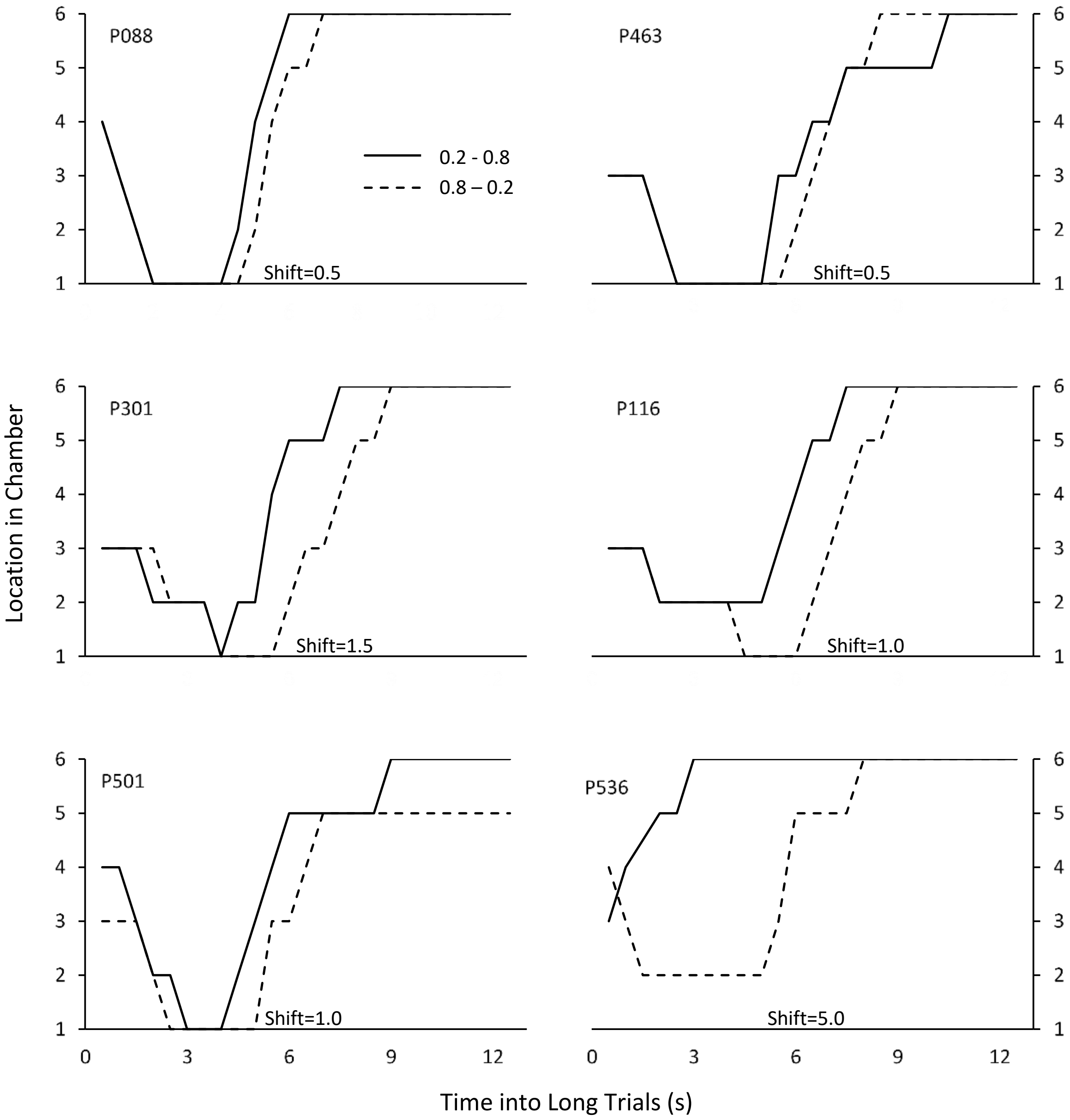

Figure 13. Median motion patterns for the test phase in conditions with differential payoff for S and L: $LB_{(0.2\text{-}0.8)}$ (solid line) and $SB_{(0.8\text{-}0.2)}$ (dashed line). The left panel shows pigeons that started on $LB_{(0.2\text{-}0.8)}$ and the right panel shows pigeons that started on $SB_{(0.8\text{-}0.2)}$. The magnitude of the shifts refers to the difference in median DT between conditions.

Figure 14 shows the average of the individual Empirical Cumulative Distribution Functions of DT. The distribution for condition $LB_{(0.2\text{-}0.8)}$ is shifted to the left, compared to $SB_{(0.8\text{-}0.2)}$, and is representative of individual subjects' performance. Birds consistently departed earlier when food was more likely on the long side (solid curve), and later when food was more likely on the short side (dashed curve). Thus, the distribution of DT, another measure of the indifference point in the bisection task (Machado and Keen, (2003), is also sensitive to differences in relative payoff. These results replicate Daniels et al.'s (2015) leftward shifts in cumulative switching points when responses to the long interval had higher payoff and extended their findings to a condition in which "short" had higher payoff.

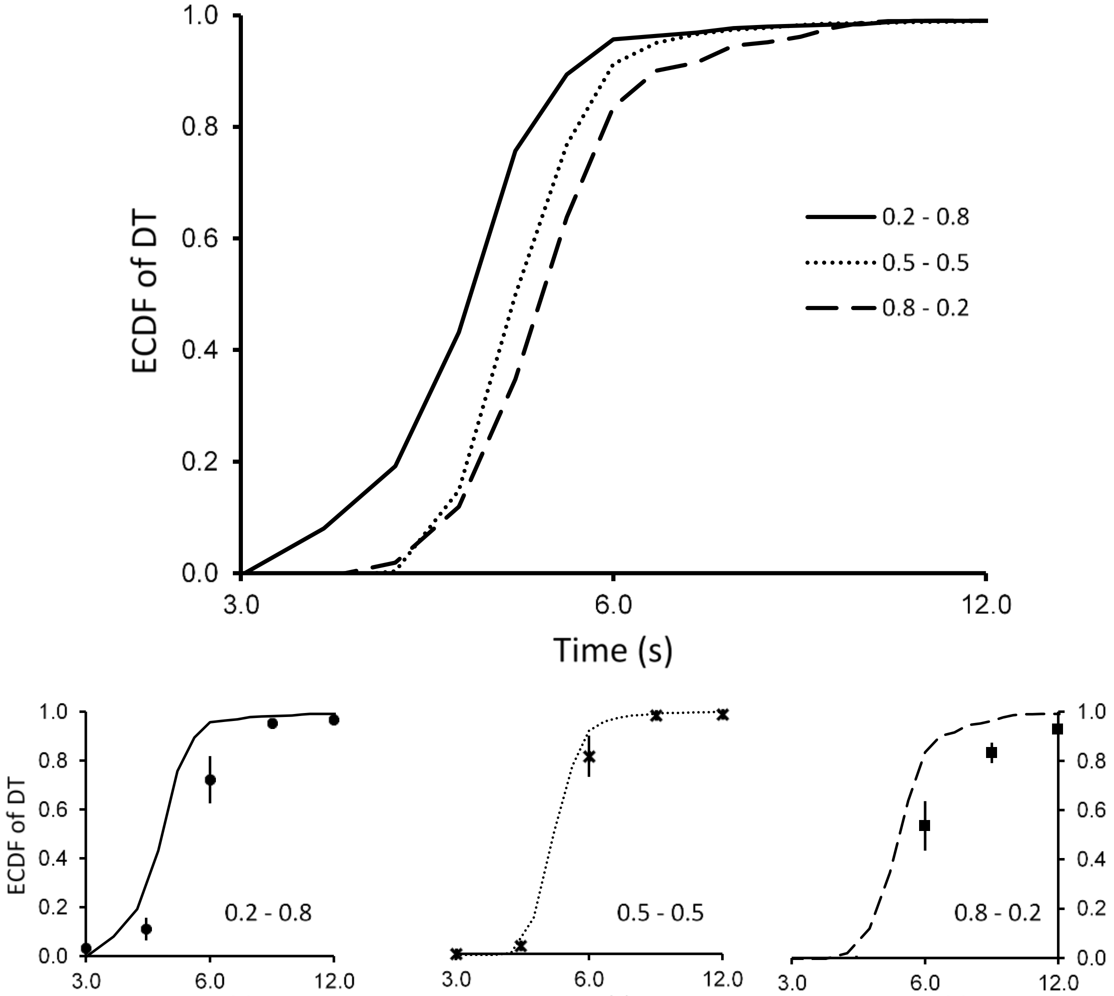

Figure 14. Top panel: Averaged empirical cumulative distribution function of departure times (ECDF of DT) in L samples for conditions $LB_{(0.2\text{-}0.8)}$ (solid line), $NB_{(0.5\text{-}0.5)}$ (dotted line), and $SB_{(0.8\text{-}0.2)}$ (dashed line). Bottom panel: ECDF of DT (lines) plotted against proportion of "long" (symbols) for conditions $LB_{(0.2\text{-}0.8)}$ (left; solid line-filled circles), $NB_{(0.5\text{-}0.5)}$ (center; dotted line-crosses), and $SB_{(0.8\text{-}0.2)}$ (right; dashed line-filled squares).

Motion and Choice. Finally, our procedure enabled us to ask: How does the distribution of departure times relate to the choice-based psychometric function? Although the direction and magnitude of the shifts are similar in the psychometric function and the distribution of departure times, the proportion of "long" choices deviated from the distribution function when $p \neq q$. The bottom panel of Figure 14 compares the two. The lines replot the average distributions, and the symbols show the average p("long") after each sample. The left, middle, and right panels correspond to conditions $LB_{(0.2\text{-}0.8)}$, $NB_{(0.5\text{-}0.5)}$, and $SB_{(0.8\text{-}0.2)}$, respectively. Visual inspection suggests that, when $\Delta = 0$ (middle), the distribution function of departure times and choice-based p("long") agree reasonably well, but when $\Delta \neq 0$ the distribution tends to overestimate p("long"). Thus DT predicts choice accurately only when there is no payoff differential.

Categorizing motion patterns. Given that the mismatch between the predicted (from the distribution of departure times) and the observed choice proportions occurred mostly for the intermediate samples, we undertook a more detailed analysis of motion during these samples. We classified the motion patterns for the 4.2, 6.0, and 8.5-s trials as follows: the pigeon moved to the (1) *short* side, and stayed there until the end of the sample (*S*); (2) *short* side first, then to the center of the chamber, and finally returned to the *short* side (*SS*); (3) *short* side first and then to the *long* side (*SL*), or; (4) *long* side and stayed there (*L*). An additional pattern (*LS*) was found exceptionally for P536, on 50% of the 4.2-s samples in condition $LB_{(0.2\text{-}0.8)}$: It moved directly to the *long* side at trial onset, but returned to peck at the "short" key after sample offset. From the baseline training data (Figure 11), we predicted a preponderance of *S* and *SL* patterns for the 4.2-s samples, and of *SL* patterns for the longer samples.

Figure 15 shows the average proportion of trials in which each pattern (except *LS*) occurred for each sample and experimental condition. The typical patterns observed during training, classified as *S* and *SL*, dominated: *S* was more frequent during the 4.2-s samples, which were below the average DT for both conditions ($LB_{(0.2\text{-}0.8)}$ = 4.94 s, $SB_{(0.8\text{-}0.2)}$ = 5.66 s; individual parameters in Appendix B, Table B2); *SL* was more frequent during the longer samples, which were close to the AT_L (in condition $LB_{(0.2\text{-}0.8)}$ arrival at *long* was between 6 s and 8.5 s (*M* = 7.19 s, *SD* = 1.96), and in $SB_{(0.8\text{-}0.2)}$ it was near 8.5 s (*M* = 8.68 s, *SD* = 1.11).

However, the payoff manipulation seems to disrupt the stereotypical patterns in some trials: After departing to the *long* side, pigeons returned to the *short* side after sample offset (pattern *SS*). In fact, the proportion of *SS* patterns is approximately equal to the difference between the distribution function and "long" proportions. We conclude that under unequal payoffs, mean DT no longer predicts choice, for the birds will occasionally choose "short" after having departed towards the *long* side of the chamber.

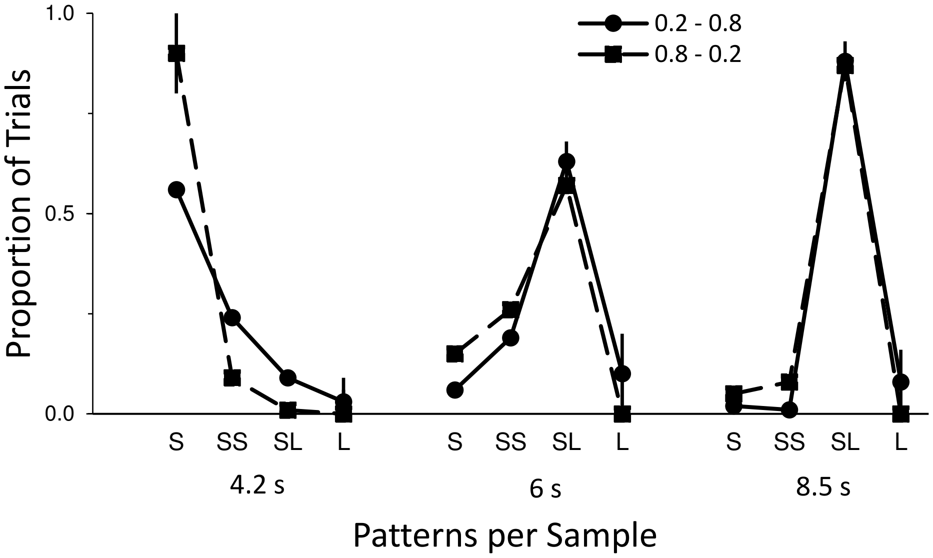

Figure 15. Proportion of motion patterns categories observed for intermediate durations during test phases of conditions LB$_{(0.2\text{-}0.8)}$ (circles), SB$_{(0.8\text{-}0.2)}$ (squares). L = Long, SL = Short→Long, S = Short, and SS = Short→Center→Short.

Location, time, and choice. The *SS* pattern suggests that choice responses may have been controlled by location as well as sample durations. Unlike Machado and Keen's (2003) task, which illuminated the side keys as soon as the sample had elapsed, in the current experiment, illumination depended on reaching locations 1 or 6. This procedural change aimed to prevent sign tracking, that is, that the pigeons approached and pecked the key that happened to be in their field of vision at sample offset, regardless of sample duration. Our preparation, however, may have increased control of choice by the location of the bird in the chamber.

To illustrate, refer to Figure 16. The grayscale gradient shows the average proportion of trials the birds were at each location as a function of time. In each panel, each vertical slice represents a spatial gradient at the corresponding time t (in 0.5-s bins). If we let p(λ|t) represent the proportion of trials the bird was at location λ given that the sample lasted t seconds, then the gray scale represents p (from 0 = white to 1 = black). The left and right panels show the gradients based on on all probe trials with samples shorter than 12 s during conditions LB$_{(0.2\text{-}0.8)}$ and SB$_{(0.8\text{-}0.2)}$, respectively.

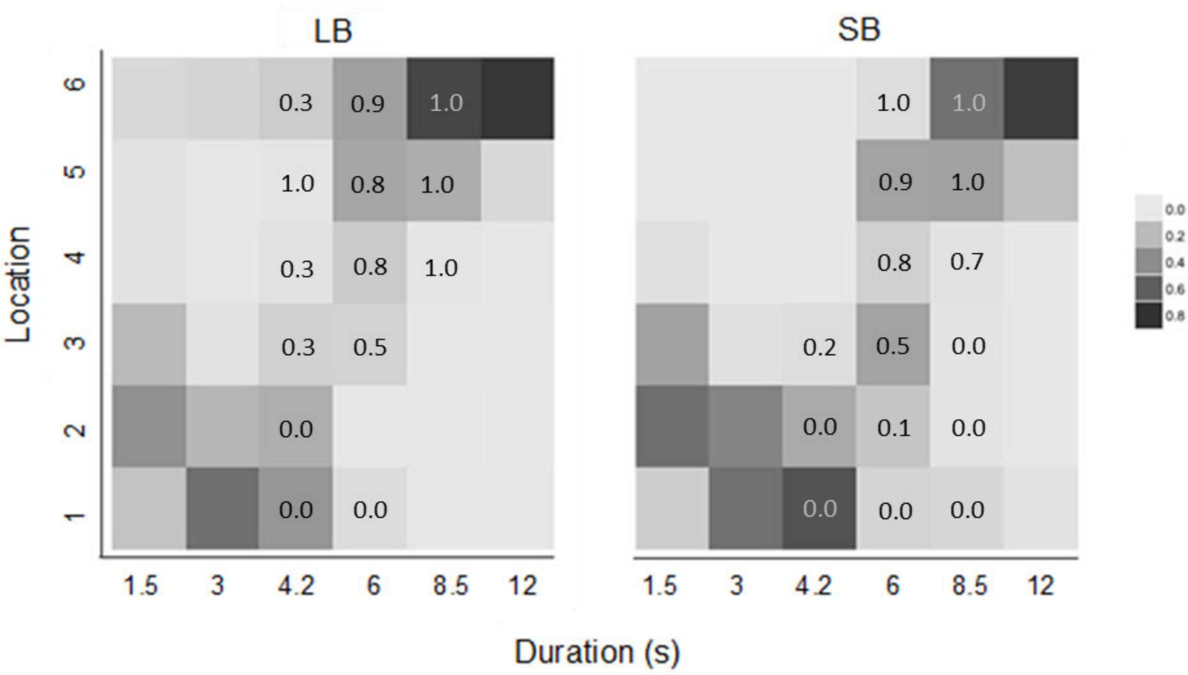

Figure 16. Average proportion of trials the birds were on each location at time of sample offset (0.5-s bins). The left and right panels correspond to the test phase of conditions $LB_{(0.2\text{-}0.8)}$ and $SB_{(0.8\text{-}0.2)}$, respectively. Values indicate the pooled proportion of "long" choices given each location, per intermediate test sample.

These two-dimensional generalization gradients reveal several effects. We see that the gradients on probe trials agree with the general motion patterns revealed by the median location curves of Figure 9. The one or two darkest squares in each column move, as it were, first to location 1 and then to location 6, staying mostly at location 1 for t = 3 s and t = 4.2 s and location 6 for t = 8.5 s and t = 12 s. By comparing the left and right panels we see that the squares at times 3.0 s and 4.2 s and locations 1 and 2 are darker in condition $SB_{(0.8\text{-}0.2)}$ than in condition $LB_{(0.2\text{-}0.8)}$. This means that the proportion of trials in the *short* side of the box is higher in condition $SB_{(0.8\text{-}0.2)}$ than in condition $LB_{(0.2\text{-}0.8)}$. Additionally, the top left quadrants ($t \leq 4.2$ s and $\lambda \geq 4$) are darker in condition $LB_{(0.2\text{-}0.8)}$ than in condition $SB_{(0.8\text{-}0.2)}$, revealing the higher proportion of trials on which the birds move directly to the L side. These are both behavioral effects of the payoff manipulation.

Most importantly, the intermediate samples show that, although modal location at t = 4.2 s was location 1, there was an appreciable probability they had already departed and were standing at locations 2 or 3 at the moment of choice. At t = 6 s, the proportions are more evenly distributed across locations and the pigeons could have been in a variety of positions at the moment of choice, although it was slightly more likely they were at the *long* side in condition $LB_{(0.2\text{-}0.8)}$. Finally, at t = 8.5 s, although pigeons had mostly arrived at location 6, on a small proportion of trials they were not at this location at the moment of choice, especially in condition $SB_{(0.8\text{-}0.2)}$.

The numbers in Figure 12 are the proportion of “long” choices given that the animals were at each location for each intermediate sample (see number of “long”/location in Appendix C). The *SS* pattern occurred when the pigeons were somewhere in the middle of the chamber ($2 \leq \lambda \leq 5$) at trial offset. The closer to the *short* side, the lower p(“long”), that is, the higher the probability that – even though they had already been at *short* and departed – they would return and choose “short”. Conversely, the closer to the *long* side, the higher p(“long”). This trend interacts with the experimental condition because when biased for long, birds are never on the *short* side at t = 8.5 s, and when biased for short, they are never on the *long* side at t = 4.2 s. Additionally, the small proportion of trials at t = 4.2 s, on $\lambda = 6$, is due to P536’s *LS* pattern. Thus, it seems that, at trial offset, the birds’ subsequent choice depends on its location in the chamber as well as on the payoff conditions.

To summarize, this account may help explain the discrepancies between p(“long”) and the distribution of departure times: The animal moves to the *short* side at the start of the trial, after more than 3 s have elapsed, it departs towards the *long* side. However, the intermediate sample offsets when the pigeon is at at a middle location (closer to *short* the shorter the sample and vice-versa), indicating the animal may receive food for key pecking (i.e., “make a decision”). The choice is then affected by payoff conditions: In No-Bias, departure time is a good predictor of choice, meaning that, if an animal has departed to long, it will, in fact, peck “long” (i.e., the distribution function of DT and proportion of “long” match). However, in Long-Bias and Short-Bias, departure time is no longer a good predictor of choice and location becomes an important source of control at sample offset, taking precedence over time.

Daniels, Fox et al. (2015; see also Daniels, Watterson, et al., 2015) have also suggested that biasing can reduce the probability that animals engage in timing. However, their model incorporates a non-timing component at trial onset, while our animals seem to start timing most trials and location gains control at sample offset, or the moment of choice.

In conclusion, this experiment enabled us to investigate the relation between motion patterns during the trial and choice at the end of the trial. The two types of analyses revealed biasing effects in the same direction and of similar magnitude. However, the distribution function of departure times did not predict accurately subsequent key-choice for durations between S and L. This discrepancy may be due to a reduction of temporal control that enabled other cues, such as location, to influence choice behavior.

General Discussion

The present study investigated the effects of differential probabilities of reinforcement for “short” and “long” responses in a bisection task. In Experiments 1A and 1B, pigeons went through a typical bisection task, learning a duration-key color mapping (e.g., S—red, L—green), before being exposed to five conditions with differential payoffs. Experiment 2 extended the previous studies to a long operant chamber, with response keys far apart and sensitive floor panels that recorded location throughout the trials. In that chamber, the pigeons learned a time-place mapping (e.g., S—left, L—right). To measure the effects of varying the payoff differential, we computed psychometric functions based on choice proportion and estimated their location and scale parameters, measures of response bias and temporal sensitivity, respectively. In Experiment 2, we also computed Empirical Cumulative Distribution Functions of Departure Times to relate the motion patterns during the sample to choice behavior after the sample.

Regarding response bias, higher payoff for “short” produced a rightward shift of the psychometric function, increasing the PSE. Conversely, higher payoff for “long” produced a leftward shift, decreasing the PSE. In Experiment 2, similar shifts also occurred on the trial-by-trial PSEs. These results were consistent throughout our study, despite the different testing strategies. However, reinforcing both anchors during testing (Experiment 1A) affected the psychometric function on the second session, whereas maintaining during testing the payoff differential used during training (Experiments 1B and 2) did not change behavior for up to six sessions. Altogether, the experiments showed differences in animals’ preference for “short” or “long” that were consistent with the relative payoff provided for each response, a bias effect.

Despite ample procedural differences, our results extend the generality of previous findings from studies manipulating differential payoffs using the FOPP (Bizo & White, 1995; Cowie, Bizo, et al., 2016; Guilhardi et al., 2007; Machado & Guilhardi, 2000), the “switching” task (Daniels, Fox, et al., 2015) and a variation of the bisection task (Stubbs, 1976). Interestingly, the only study using the standard temporal bisection task (Galtress & Kirkpatrick, 2010) failed to obtain consistent shifts in PSE between different payoff conditions. However, the study manipulated the magnitude of reinforcement following “short” and “long” correct choices (i.e., number of pellets).

Our manipulation was more like the FOPP studies, which provided reinforcers intermittently. Studies have indicated that multiple dimensions of a reinforcer can modulate operant behavior. For instance, there is evidence that magnitude manipulations tend to have a smaller effect on choice than rate-based manipulations (Elliffe, Davison, & Landon, 2008). Also, decreasing the likelihood of a reward seems to increase variability (e.g., Stahlman, Roberts, & Blaisdell, 2010), while increasing reward magnitude has the opposite effect (e.g., Stahlman & Blaisdell, 2011). Shifts in the PSE could be more likely when behavior remains variable, for instance when the timed intervals are more difficult to discriminate, or when reinforcement delivery is less predictable.

Unlike the FOPP or Stubbs' (1976) procedure, the standard bisection is a two-part procedure with a training and a testing phase. The main challenge for this study was how to maintain similar conditions across the tests (Experiment 1A) or during training and testing (Experiments 1B and 2). We found that proportion of "long" covaried only with the sign, but not the magnitude, of Δ even when overall reinforcement probability (O) remained constant. Only two previous studies investigated responding for a range of payoff values for short and long intervals. Stubbs (1976) and Bizo and White (1995) both observed that the magnitude of the shifts depended monotonically on the difference between the payoffs for the S and L samples, or the first and second trial halves, respectively. While these studies did not alter O between conditions, in Experiment 1, O may have had a role in modulating the biasing effects of Δ (Machado & Keen, 1999; Machado et al., 2008)

Although studies using the FOPP (Bizo & White, 1995; Cowie et al., 2016; Guilhardi et al., 2007; Machado & Guilhardi, 2000) found larger shifts in response functions compared to ours, it is likely that the expression of time-controlled behavior is related to differences between tasks. For example, in the bisection task, reinforcers interact differently with temporal control because they are only delivered at the end of the timed interval. In the FOPP, the presence of reinforcers during the interval could lead to more immediate and visible effects on temporally controlled behavior (Cowie, Davison, Blumhardt, & Elliffe, 2016).

It is also worth noting that in the FOPP trial durations are typically much longer than in the bisection task. In Machado and Guilhardi (2000), the psychometric functions shifted on average 12 s in 50-s trials (approximately 20%), for a three-fold difference in payoff between the first (short) and second (long) halves. In the present studies, the average shifts were no greater than 3.5 s, even though payoffs were up to ten times higher for a given response.

Daniels, Fox, et al. (2015) also found shifts ranging from 1 to 3 s for a 16-s long FI. It has been suggested that shifts in psychometric functions are proportional to the duration being timed (Meck, 1996), which would be consistent with the scalar property of timing (Gibbon, 1981). However, this conjecture remains to be tested within the same preparation.

Together with the temporal generalization procedure, the temporal bisection procedure is a retrospective timing task. Behavior is measured only after the sample and few responses are collected per sample – few, that is when compared with the number of responses collected in concurrent timing tasks such as the FOPP, the FI, or the peak procedure. Per force, the psychometric functions obtained in the bisection task rely on a relatively small number of choices. Changing the task to a time-place learning task, with the choice alternatives apart and the ability to track the subject's motion during the sample, eliminates some of the shortcomings of the standard bisection task. In the new task, each L trial yields a PSE in addition to the choice data. Recording the displacements during the sample in Experiment 2 changes the bisection task into a concurrent timing task by "externalizing," so to speak, hypothetical internal constructs (e.g., internal clock).

Experiment 2 brought to light the relationship between motion patterns during the trial and final choice in a bisection task. Similar to the effects observed in the psychometric functions of all experiments, the empirical cumulative distribution function of departure times too, was horizontally displaced, as expected from the payoff manipulation. Yet, these same distribution of departure times did not predict choice accurately, probably because differential payoff reduced the temporal control and increased location control over the behavior at sample offset. Perhaps future studies could see whether other measures (e.g., the amplitude of the motion, i.e., the distance from x(t = sample offset) to x(t = ATs)), correlate better with choice proportion. Recent research has also supported a notion of time as a stimulus dimension that competes with other dimensions such as color or location for the control over behavior (for a review, see Mcmillan, Spetch, Sturdy, & Roberts, 2017). Timing models that consider these processes may have a predictive advantage over those that do not (e.g., Cowie, Davison, & Elliffe, 2014; Daniels, Fox, et al., 2015).

Despite some inconsistencies across tasks and studies, results point towards changes in psychometric functions based on differential reinforcement for responding during, or after, short *versus* long intervals of time. Some timing models, such as Learning-to-Time (LeT; Machado, 1997a; Machado et al., 2009) and the Behavioral Economic Model (BEM; Jozefowiez et al., 2009), predict a bias effect for differential rates of reinforcement, a result observed in a broad range of tasks. To date, this bias had not been documented in the standard bisection task with non-human animals (for an example with humans, see Akdoğan & Balcı, 2016). The Scalar Expectancy Theory (SET; Gibbon, 1977, 1981) on the other hand, does not predict biased performance without further assumptions (but see the "modified Church and Gibbon" model; MCG; Wearden, 1992). On the other hand, none of these models predict changes in sensitivity between baseline and differential payoff conditions, nor between Long-Bias and Short-Bias conditions.

The payoff manipulations for all our experiments failed to produce systematic changes in sensitivity, whether the overall rate of reinforcement remained constant across conditions (Experiment 2) or not (Experiments 1A and 1B). This result is consistent with Bizo and White (1995), and Machado and Guilhardi (2000). In contrast, Cowie et al. (2016) found that differential reinforcement increased sensitivity when the second half of each FOPP trial yielded a higher payoff and decreased it when it yielded a lower payoff. This finding was attributed to a concentration of obtained reinforcers especially at the beginning of the first half of the trials. However, the dynamic interaction between choice and obtained reinforcers in their task was not different from the typical FOPP and thus would not explain why other experiments found no differences in sensitivity across conditions. More importantly, no such interaction occurs in the bisection task because reinforcers are not delivered throughout trials, as in the FOPP, but only at the end of the sample.

Interestingly, Galtress and Kirkpatrick (2010) found a flattening of the psychometric function in rats whenever conditions of differential payoff were in effect. Daniels, Fox, et al. (2015) also found a decrease in sensitivity for rats and humans, but no change for pigeons. In both cases, the authors hypothesized that the flattening might have been caused by decreased temporal control by the samples (or "attention" to time) induced by the increase in overall reinforcement. However, there is no evidence of similar findings in pigeons. Additionally, rats seem to produce overall flatter psychometric functions than other species: Functions reported by Guilhardi et al. (2007) with rats were flatter than the ones found in Machado and Guilhardi's (2000) original study with pigeons. Daniels, Fox, et al. (2015) also showed overall flatter functions for rats when compared to pigeons or humans. Differences between species' may preclude general conclusions about the effects of differential reinforcement on the temporal regulation of behavior, even in putative similar tasks. Future comparative studies should examine whether the small differences in procedural adaptations to a species are responsible for differences in the results.

The present study confirmed that control of temporal behavior depends on differences in relative reinforcement between the short and long sample stimuli in a bisection task. The distribution of reinforcers in a session did not produce significant changes in sensitivity, but biased choice and departure times, in addition to reducing overall temporal control. However, the mechanisms behind these effects remain unclear. Models of timing that consider response bias, as well as competition between time and other stimulus dimensions, should predict behavior better under conditions of differential payoff.

CHAPTER III[2]

DIFFERENTIAL BASE-RATE EFFECTS ON PIGEONS

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[2] This Chapter reproduces the submitted version of the paper:

Cambraia, R., Vasconcelos, M., Jozefowiez, J. & Machado, A. (2019). Base-rates Bias Performance in a Temporal Bisection Task. *Manuscript submitted for publication.*

I would like to thank Catarina Vila Pouca for collecting data for Experiment 1 and Nicole Sobral Félix for help collecting data for Experiment 2.

Abstract

We investigated how differential base-rates affect temporal discrimination. In a temporal bisection task, pigeons learned to choose one key after a short sample and another key after a long sample. When presented with a range of intermediate samples they produced a Gaussian psychometric function characterized by a location (bias) parameter and a scale (sensitivity) parameter. When one of the trained samples was presented more frequently than the other, the location parameter changed, with the pigeons biasing their choices toward the key associated to the most frequent frequent sample. We then reproduced the bisection task in a long operant chamber, with choice keys far apart, and tracked the pigeons' motion patterns during the sample. Pigeons learned to approach the short key following sample onset, remain for a few seconds, then depart towards the long key. Location in time was also affected by unequal base-rates. The likelihood of pigeons going directly to the long side soon after sample onset increased when long samples were most frequent, indicating a decrease of temporal control. We found no evidence of changes in temporal sensitivity. The results are most consistent with models of timing that take into account bias effects and competition of stimulus control.

In the study of stimulus perception, researchers have traditionally manipulated the frequency of stimulus presentation – base-rate –, or of reinforcement associated with these stimuli – payoffs –, mostly under a Signal Detection Theory paradigm (Green & Swets, 1966). Only towards the late 20th century have researchers shown increasing interest in studying how these and other non-temporal factors affect temporal discrimination (Balcı, 2014; Fayolle, Lamotte, Droit-Volet, & Gil, 2013; Galtress et al., 2012; Killeen & Fetterman, 1988; Machado et al., 2009; Meck, 1996).

Payoff manipulations in temporal discrimination procedures have focused on how reinforcers bias responding (e.g., Bizo & White, 1994b, 1994a, 1995; Galtress & Kirkpatrick, 2009; Machado & Guilhardi, 2000; Morgan et al., 1993; Raslear, 1985; Roberts, 1981; Stubbs, 1976) and, at times, affect sensitivity to timed stimuli (e.g., Bizo & White, 1994a; Cowie, Bizo, et al., 2016; Galtress & Kirkpatrick, 2010). Base-rate, however, has been less explored in interval timing experiments, even though it could be considered functionally similar to reinforcement contingencies (i.e., payoffs) in determining choice behavior (Catania, 1966; Nevin, 1969).

A common procedure used to study the relation between stimulus presentation and temporally controlled responding is the bisection task (Church & Deluty, 1977). In this task, a sample stimulus (e.g., a houselight) is presented in discrete trials for either a short (S) or a long (L) duration (e.g., S = 3 s and L = 9 s). Then, the subject chooses between two operanda, say, a left lever and a right lever; one choice is rewarded following S, and the other following L. After the animal learns the two sample-response mappings, the experimenter introduces test samples with intermediate durations and records the proportion of “long” responses (i.e., choices of the lever rewarded following L) after each sample.

Typically, the proportion of “long” responses increases with sample duration from approximately zero to approximately one. The resulting sigmoidal psychometric function has two important properties that characterize performance: The moment the function crosses the indifference line and the slope of the function at that crossing point. The former is the function’s *location* parameter, usually called the Point of Subjective Equality or PSE, and measures bias. Thus, if a function is shifted leftward, i.e., more “long” choices, compared to a baseline, the PSE decreases. Rightward shifts, i.e., more “short”, mean longer PSEs. The latter is the *scale* parameter, and measures sensitivity to stimulus durations (Blough, 1958; Gibbon, 1981). The lower the values (i.e., flatter functions) the lower sensitivity to time.

This task is extremely well suited to study temporal responding under differential base-rates because one of two intervals can easily be made more prevalent. For instance, Jozefowiez, Polack, Machado & Miller (2014) examined the effects of base-rate on human temporal judgments using a temporal bisection task with S = 1 s and L = 1.5 s. Participants were assigned to either a No-Bias group or to groups that differed in the relative number of presentations of Short and Long trials: Long-Bias (twice as many L than S trials) and Short-Bias (twice as many S than L trials). During testing with intermediate durations, Long-Bias participants responded more “long” overall, shifting the psychometric function to the left of the No-Bias function, resulting in a lower PSE. Short-Bias produced a rightward shift, with fewer “long” choices (and thus a higher PSE). Çoşkun et al. (2015) replicated these results with a broader range of differential base-rate values and found that the PSEs monotonically decreased with an increase in the proportion of L trials.

Similarly, Akdoğan and Balci (2016a) trained mice to discriminate between 3 s (S) and 9 s (L) samples. After training and testing with equal base-rates, animals went through two biasing conditions in counterbalanced order, in which S trials were four times as frequent as L trials and *vice versa*. Subjects consistently produced more “long” responses when L trials were more likely (leftward shift) and more “short” responses when S trials were more likely (rightward shift).

The base-rate manipulation for short and long trials has been expanded to a “switch task” with mice (Balcı, Freestone, & Gallistel, 2009; modified from Platt & Davis, 1983). This task, like the temporal bisection task, consists of presenting intervals on discrete trials. However, here comparisons are available from the trial onset so that subjects can (and do) respond during sample presentation. Animals start responding “short” and after some time switch to “long.” Because switches occur on most trials, and behavior is tracked throughout the duration of the trials, intermediate durations are typically not presented. Mice and humans produced earlier switch-times when long trials were presented more often and later when they were less frequent, i.e., left and rightward shifts in distributions, respectively (Balcı et al., 2009).

The small shifts in the PSE found in these experiments have been well described by associative timing models (Jozefowiez, Cerutti, & Staddon, 2005; Jozefowiez et al., 2014). The effects of base-rate on time-based behavior warrants further investigation because many accounts of timing are strongly based on associative learning. The sample intervals indicate which discriminative stimulus (i.e., response key) will produce reinforcers after a given choice. While it has been suggested that interval timing underlies associative learning (Balsam, Drew, & Gallistel, 2010; Balsam & Gallistel, 2009; Gallistel & Gibbon, 2000)**,** other researchers have proposed that it is associative learning that underlies timing (Jozefowiez et al., 2009; Machado, 1997b; Machado et al., 2009)**.** In any case, the association between the presentation of stimuli of different durations and responding can be as important as the association between responses and their consequences (payoffs).

In the present study, we revisited the temporal bisection task to examine how differential probabilities of short and long samples affect time perception as represented by the psychometric function of pigeons. We also try to generalize results from previous studies, which used continuous reinforcement, to a setting in which reinforcement is presented intermittently for correct responses. Although reducing overall reinforcement could produce transient changes in timing (Bizo & White, 1994a), it should not affect later phases of the experiment, and our results should be replicate previous studies.

Consider s and l to be the probabilities of presentation of the S and L samples, respectively, with Δ as the base-rate differential (i.e., $\Delta = s - l$). Note that Δ depends exclusively on the base-rate probabilities of the two training samples and that $s + l = 1.0$. Across conditions, we varied Δ and checked for effects on the psychometric function (i.e., bias and sensitivity). To obtain the psychometric function, we presented new sample-durations during generalization tests. These tests could be conducted in a variety of ways to isolate the effects of Δ. In Experiment 1A, we eliminated the differences in base-rates used in training (i.e., train with Δs $\neq 0$, but always test with $\Delta = 0$) to maintain the test setting for all conditions, and in Experiment 1B we maintained the Δs from training to testing. In Experiment 2, the intermediate samples, or probes, were greatly outnumbered by the trained samples, so that training and testing phases were similar, as well as overall reinforcement between conditions.

In Experiment 2, we were also concerned with our subjects' behavior during the sample. Pigeons performed the bisection task in a long operant chamber where key choices were location-based, i.e., left or right, and floor panels recorded location through time. This "time-place learning task" (Wilkie & Willson, 1992) is a hybrid procedure that brings together the typical bisection task and the switch task, by recording both choices following a range of intervals and location during the trials. Much like the switch task, pigeons typically move to the *short* (e.g., left) side at sample onset, stay on that side past the duration of the S sample, and depart to the *long* (e.g., right) side on long-sample trials (Cambraia, Vasconcelos, Jozefowiez, & Machado, 2019; Machado & Keen, 2003). The parameters of these motion patterns (e.g., mean time to depart, or switch, to the *long* side) may yield behavioral measures more sensitive to base-rate than choice proportion.

With this set of experiments, we aim to understand how the base-rate differential affects temporal discrimination by assessing bias and changes in sensitivity in psychometric functions. To do so, we observed how pigeons behave both during (i.e., motion patterns) and after (i.e., proportion of "long" choices) the sample intervals in a temporal bisection task.

Experiment 1A

In Experiment 1A we varied Δ during the training conditions but always tested with same Δ = 0; moreover, untrained samples were never reinforced. We reasoned that, if learning during test sessions is relatively slow, testing under the same conditions better isolates the effects of training under different Δs. However, because learning is likely to take place during testing, prolonged exposure to the test conditions would eventually eliminate the effects induced during training. Therefore, we limited testing to three sessions after each base-rate condition.

Method

Subjects. Seven pigeons (*Columba livia*) maintained at 80% of their free-feeding weight participated in the experiment. Six subjects had previous experience with choice procedures, including timing tasks, and one was naïve. Water and grit were continuously available in their home cages. The pigeons were individually housed in a colony room with controlled temperature (between 20º and 22º C) and a 13:11h light:dark schedule with lights on at 8:00 A.M.

Apparatus. Four identical Lehigh Valley® operant chambers for pigeons were used. Each chamber was 34 cm x 35 cm x 31 cm (height x length x width). They had aluminum walls and ceiling aluminum, and the floor was a wire mesh. Centered on the back wall of the chamber, 4 cm below the ceiling, a 28-V, 0.1-A houselight provided general illumination. The response panel contained three circular keys, 2.5 cm in diameter, arranged in a horizontal row, 22.5 cm above the floor and 9 cm apart, center to center. Reinforcement consisted of mixed grain delivered by a hopper that was accessible through a 6 cm x 5 cm (width x height) opening, centered horizontally on the response panel, 8.5 cm above the floor. A 28-V, 0.04-A white light illuminated the opening whenever a reinforcer was available. An outer box equipped with a fan, for ventilation and masking outside noises, enclosed the experimental chamber. A personal computer equipped with Whisker software (Cardinal & Aitken, 2010) and running a custom written Microsoft Visual Basic 2008 program controlled all experimental events and recorded the data with a temporal resolution of 1 ms.

Procedure. The naïve pigeon (P547) learned to peck the keys via an autoshaping procedure. Then, all pigeons were required to peck at each of the side keys (red and green hues) under a Fixed-Ratio 5 schedule, during five sessions of pre-experimental training.

Following pre-training, pigeons were exposed to a temporal bisection task. All trials followed the same general structure: After a 20-s dark inter-trial interval (ITI), the houselight and the center key (white hue) illuminated simultaneously. After the sample interval elapsed, the houselight and the white center key turned off and the side keys turned on, each with a different hue, red or green. A single peck at one of the illuminated side keys turned them off and, if the choice was correct, the pigeon had access to grain. The duration of access to grain varied across birds from 3 to 5 s. It was adjusted for each bird during the first sessions to minimize extra-session feeding. After the reinforcer, the ITI followed. If the choice was incorrect, the ITI followed immediately. The position of the green and red key colors varied randomly across trials with the constraint that, at the end of each session, each color had appeared equally often in each position. For three pigeons (P726, P746, P851), choosing the red key after Short samples and the green key after Long samples were considered correct responses; for the other four (P547, P730, P752, P917) the reverse assignment was in effect. For generality, we will refer to the trained Short (S) and Long (L) samples together as anchors and to the corresponding choices as “short” and “long.”

***Discrimination Training*. S**ample intervals were 3 s (S) or 9 s (L).Initially, all trials were baited, that is, all trials were reinforced provided the choice was correct. Incorrect responses repeated the trial (correction procedure). In the first session, a single error led to a forced trial in which only the correct comparison key illuminated after the sample. In the second session, forced trials occurred after two consecutive errors. From the third session onward, the pigeon had to make three consecutive errors to start a forced trial. Sessions comprised 60 randomly intermixed trials (30 S, 30 L), excluding correction trials (see Table 4, row 1). Training continued, for a minimum of 15 sessions, until the birds met the learning criterion of 70% correct choices per sample for five consecutive sessions. Because P851 showed difficulty in reaching the learning criterion (32 sessions), we eased the discrimination by using a short signal of 1.5 s, and gradually increasing it to 3 s (steps of 0.5 s, one session with at least 70% correct per sample to increase).

Table 4

Number of Trials per Type (Short, Long, or Probe) and Corresponding Base-rates and Payoffs for Experiment 1A During Training and Test Phases of Each Condition

Condition	Phase	Number of Trials			Base-rate		
		S	L	Probe	s	l	Δ
	Discrimination Training	30	30	-	.50	.50	.00
		48	48	-	.50	.50	.00
	Generalization Test	36	36	36	.50	.50	.00
LB$_{(0.1-0.9)}$	Training	12	108	-	.10	.90	-.80
	Test	36	36	36	.50	.50	.00
LB$_{(0.2-0.8)}$	Training	24	96	-	.20	.80	-.60
	Test	36	36	36	.50	.50	.00
NB$_{(0.5-0.5)}$	Training	60	60	-	.50	.50	.00
	Test	36	36	36	.50	.50	.00
SB$_{(0.8-0.2)}$	Training	96	24	-	.80	.20	+.60
	Test	36	36	36	.50	.50	.00
SB$_{(0.9-0.1)}$	Training	108	12	-	.90	.10	+.80
	Test	36	36	36	.50	.50	.00

Next, we added extinction trials to reduce the proportion of baited trials to .67 (to match the overall proportion of reinforcement in the upcoming test). Consider the second row of Table 4 (Discrimination Training): At the beginning of each session the computer selected 32 of the 48 trials of each type (S and L) randomly and baited them. If the pigeon made a correct choice on those trials, it received food; on the remainder 16 non-baited trials, the pigeon did not receive food, even if it chose correctly. When the birds met the learning criterion (70% correct choices per sample) for three consecutive sessions, they advanced to the test phase. We removed the correction procedure for the remainder of the experiment.

Generalization Test. This phase consisted of three sessions with 108 trials each; 72 were baited trials with the anchor durations, 36 S and 36 L, and 36 were unreinforced trials (probes) with three new sample durations: 3.95, 5.20, and 6.84 s, each presented 12 times. Overall, 67% of trials were baited. Together with the 3-s and 9-s anchors, these durations form a geometric series with an approximate ratio of 1.32; the 5.20 s duration corresponds to the geometric mean of the two anchors.

***Base-rate Training*.** The subjects went through five experimental conditions (Table 4) according to a Latin square design. Given that there were seven animals (and five trial orders), two of the orders were run by two pigeons, while one bird each ran the remaining three orders. Experimental conditions differed only in the base-rate probabilities, s and l, which

Table 7either favored the short samples (Short Bias, SB), the long samples (Long Bias, LB), or none (No Bias, NB). For example, in Condition $LB_{(0.1\text{-}0.9)}$, only 10% of the trials were short (i.e., 12 S) whereas 90% of the trials were long (i.e., 108 L). Conversely, in Condition $SB_{(0.9\text{-}0.1)}$, 90% of the trials were short (i.e., 108 S) whereas only 10% of the trials were long (i.e., 12 L). Two out of three trials per sample were baited (67%). Training was in effect for five sessions and comprised 120 trials. A test phase followed each training phase.

***Base-rate Test*.** The Base-rate Test phase was the same as described for the Generalization Test and occurred immediately after each Base-rate Training.

Results and Discussion

All pigeons learned the bisection task. When 100% of the trials were baited, they required on the average (range) 22.4 (15 – 46) sessions to meet the learning criterion; when only 67% of the trials were baited, they required 6.1 (5 – 10) additional sessions to meet the criterion. At the end of training, the proportion of correct responses averaged .91 (.78 – 1.00) for S and .90 (.78 – .97) for L, $t(6) = 2.45$, $p = .39$.

To characterize the individual psychometric functions, we fit each of them with a two-parameter cumulative Gaussian distribution function by the method of least-squares. The best-fitting location parameter, μ, estimates the point of subjective equality (PSE). The best-fitting scale parameter, σ, estimates sensitivity to sample duration: σ is inversely proportional to the slope of the function at the PSE, with larger values (flatter functions) indicating lower sensitivity. Appendix D, Table D1, lists the best-fitting parameters and R^2 as an indicator if the goodness of the fit.

In the Generalization Test, the average PSE equaled 5.41 s (*SEM* = ±0.22), a value greater than the geometric mean (5.2 s) but less than the arithmetic mean (6 s) of the trained durations. The scale parameters averaged 1.71 (*SEM* = ±0.22). Results are typical of the bisection task with non-human animals (e.g., Catania, 1970; Church & Deluty, 1977; Fetterman & Killeen, 1991; Killeen & Fetterman, 1988; Machado, 1997; Morgan, Killeen, & Fetterman, 1993; Platt & Davis, 1983; Stubbs, 1968).

Figure 17 shows the average psychometric function (symbols). As expected, the proportion of "long" responses increased smoothly as a function of sample duration; choice following the trained samples remained accurate during testing (see filled and empty circles at 3- and 9-s samples). The curve through the data points shows the average of the individual best-fitting functions. The fitted functions accounted well for the observed proportion of "long" (R^2: $M = .98$, $SEM = 0.05$).

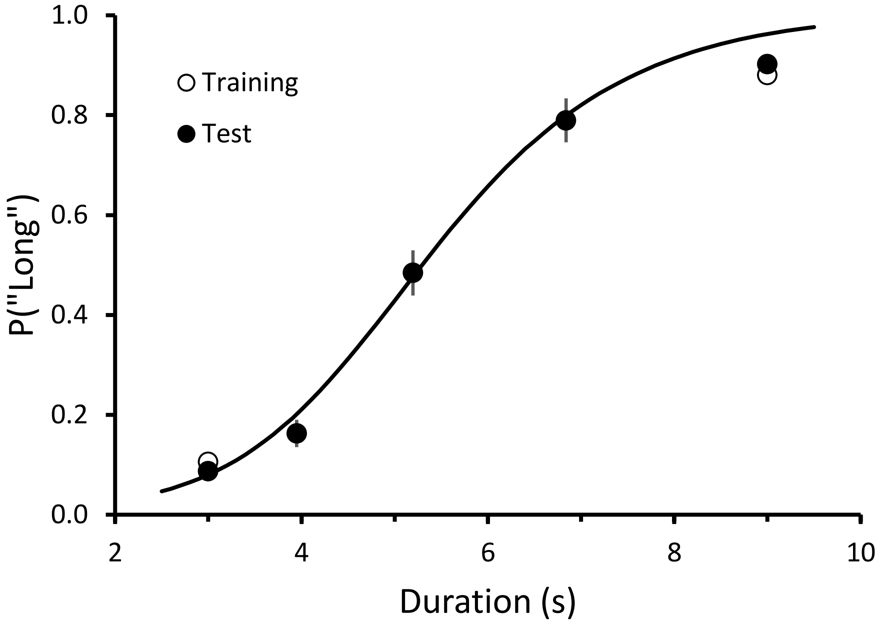

Figure 17. Proportion of "long" responses (*M* ± *SEM*) as a function of stimulus duration obtained in the Generalization Test (filled circles) and curve with averaged parameters from individually- fitted cumulative Gaussians (solid line) in Experiment 1A. Unfilled circles show the average proportion of "long" responses for the last five sessions of Discrimination Training.

The biasing effects of Δ are displayed in Figure 18, where the average psychometric functions from each condition are plotted for the three test sessions (Test 1-3). In Test 1 (top panel), when L was most likely to occur (filled data points), the preference functions are shifted leftward, whereas when S was most likely the functions are shifted rightward. Performance for the anchor durations remained generally high, except for S, in condition $LB_{(0.1\text{-}0.9)}$, and L, in both SB conditions. A repeated-measures ANOVA confirmed significant main effects of condition, $F(4, 24) = 7.81$, $p < .001$, $\eta_p^2 = .565$, and sample duration, $F(4, 24) = 142.16$, $p < .001$, $\eta_p^2 = .960$. Conditions with the same absolute value of Δ interact with duration in interesting ways, $F(16, 96) = 1.95$, $p = 0.025$, $\eta_p^2 = .245$. While conditions with the largest absolute value, i.e., $\Delta = \pm 0.8$, are more shifted for shorter sample intervals, $\Delta = \pm 0.6$ (squares) are more shifted for longer samples.

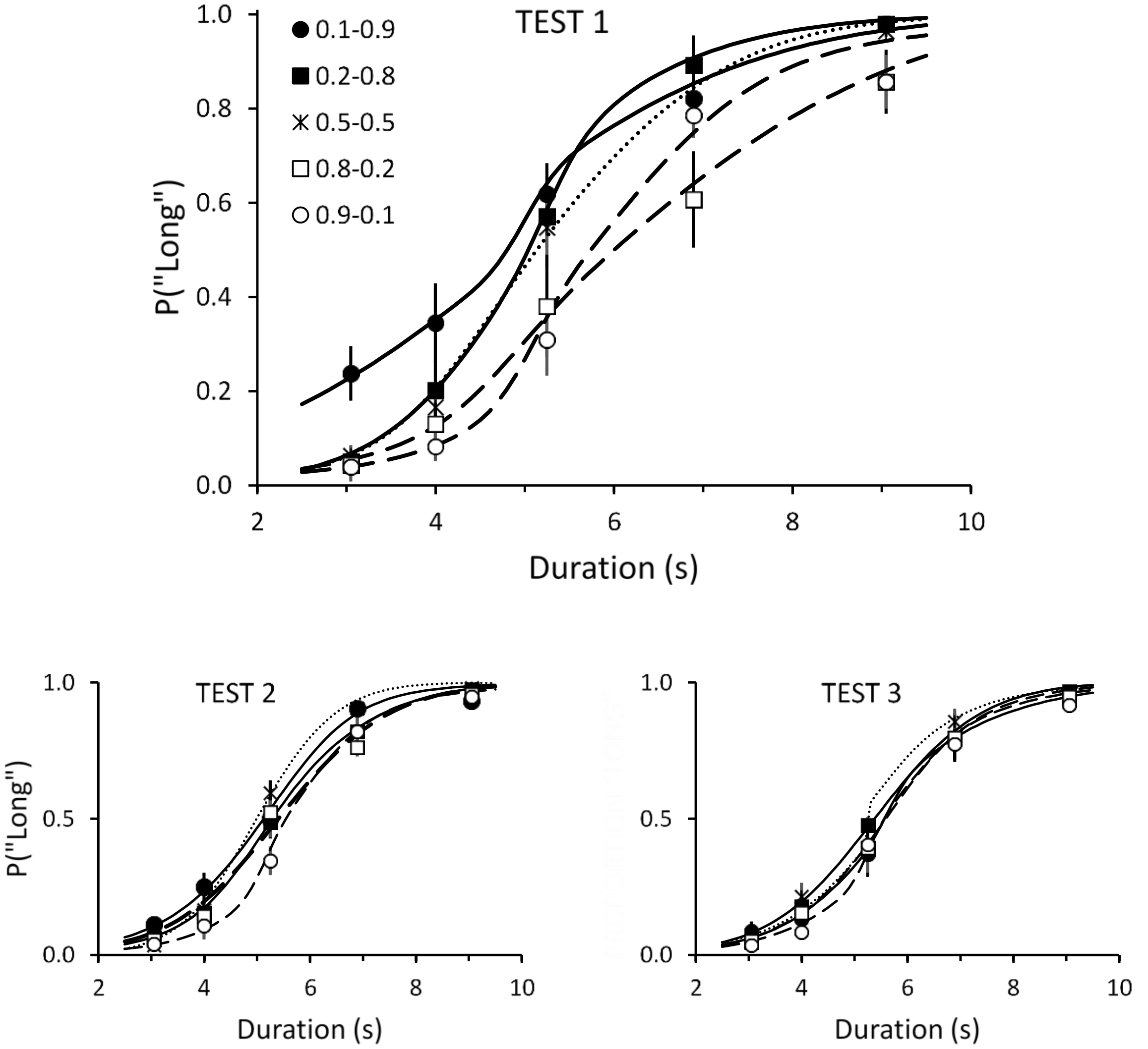

Figure 18. Proportion of "long" responses (M ± SEM) for each condition: $LB_{(0.1\text{-}0.9)}$ (solid circles), LB($_{(0.2\text{-}0.8)}$ (solid squares), $NB_{(0.5\text{-}0.5)}$ (asterisks), $SB_{(0.8\text{-}0.2)}$ (empty squares) and $SB_{(0.9\text{-}0.1)}$ (empty circles), and corresponding curves with averged parameters from individually fitted cumulative Gaussians (solid lines for LB, dashed lines for SB, dotted line for NB), in Experiment 1A. Top panel shows first test session, bottom panel shows second (left) and third (right) test sessions. NB = No-Bias, LB = Long-Bias, SB = Short-Bias.

Performance was affected by testing: As test sessions ($s = l$) progressed, the functions shifted closer together, decreasing the effect of condition produced by previous training with $s \neq l$. While Test 2 (bottom left panel) shows a smaller, yet still significant effect of condition, with a smaller effect size, *F*(4, 24) = 3.01, $p = .038$, $\eta_p^2 = .334$; by Test 3 (bottom right panel), the functions are no longer significantly shifted, *F*(4, 24) = 0.68, $p = .614$, $\eta_p^2 = .101$. Birds remained sensitive to duration, *F*(4, 24) = 219.97, $p < .001$, $\eta_p^2 = .973$. Because the biasing effect was most prominent in the first session, we restricted parameter analyses to Test 1.

Figure 19 shows the average location (μ; top panel) and scale (σ; bottom panel) parameters from the individually fitted cumulative Gaussian distribution functions in Test 1 (for individual best-fitting parameters, see Appendix D, Table D1). The dotted horizontal lines indicate the average value from the Base-rate Test. Because P917 produced a very long PSE (μ) in $SB_{(0.8\text{-}0.2)}$, the empty circle indicates the data point excluding this outlier. The location parameter differed significantly across conditions, *F*(4, 24) = 5.67, $p = .002$, $\eta_p^2 = .486$, and generally shows the expected trend, i.e., increased as the base-rate differential (Δ) increased. The scale parameters did not differ significantly across conditions, *F*(4, 24) = 1.36, $p = .277$, $\eta_p^2 = .185$. In short, bias varied systematically with Δ, but sensitivity to stimulus duration did not.

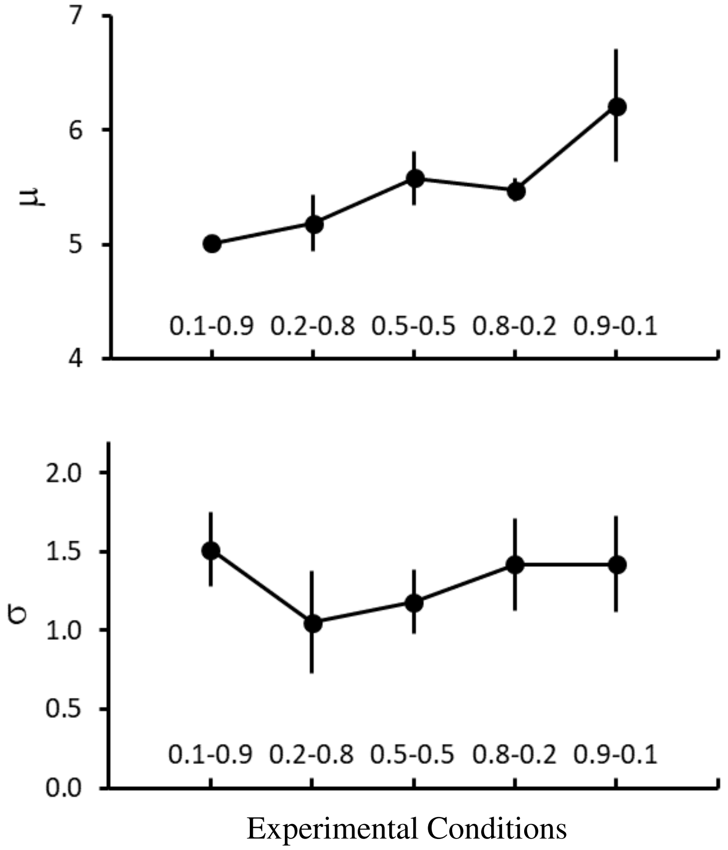

Figure 19. Parameters per condition (*M* ± *SEM*) from individual cumulative Gaussian fits: μ (top), σ (bottom) of Experiment 1B.

Although previous studies have manipulated the sign of Δ by presenting either more S or more L-sample trials (Akdoğan & Balcı, 2016a; Jozefowiez et al., 2014), only two studies had more than one positive and negative Δ value. Both Balcı et al. (2009) and Çoşkun et al. (2015) observed that mean PSEs increased monotonically as a function of Δ, but neither analyzed sensitivity to time. In the current study, PSEs increased as Δ increased, although the overall functions seem to interact with sample duration; sensitivity was unaffected by Δ.

Experiment 1B

In Experiment 1A, training with differential base-rates and testing with equal base-rates, i.e., $\Delta = 0$, maintained testing conditions throughout the experiment. However, exposure to testing with $\Delta = 0$, and payoffs for the anchors increasing to 1.0 from training to testing meant the effect quickly disappeared. In Experiment 1B, the base-rate differential used during training remained in effect during testing. Non-differentially reinforcing the intermediate durations maintained payoffs for S and L equal from training to testing, while also maintaining the overall rate of reinforcement throughout the experiment. It also allowed us to observe whether the base-rate effect remained conditions similar to those used in experiments manipulating payoff (Cambraia et al., 2019; Stubbs, 1976).

Method

Subjects and Apparatus. The same seven pigeons from Experiment 1A participated in this experiment. Housing conditions and apparatus remained as in Experiment 1A.

Procedure. ***Base-rate Training.*** The base-rate conditions (Table 5) were the same as in Experiment 1A, with trials and sessions following the same structure. Order of conditions for each bird also remained the same. The criterion to advance to the test phase was a stable performance for three consecutive sessions, with a minimum of five and maximum of ten sessions per condition.

Base-rate Test. The base-rate differential, Δ, was the same in training and testing (Table 2). Responses to probes were partially reinforced regardless of choice (at the same probability as the anchors, .67), to maintain anchor payoffs equal from training to testing, while also keeping the overall rate of reinforcement constant throughout the experiment. Test sessions comprised 96 trials each: 60 anchors and 36 probes. Probe durations remained the same: 3.95 s, 5.20 s, and 6.84 s. Testing ended after 3 test sessions.

Transition. Because testing now maintained the Δ from training, the experimental conditions were separated by a transition phase to reduce potential carry-over effects. Transition consisted of a minimum of three training sessions equal to the No-Bias condition, NB$_{(0.5-0.5)}$. To advance, birds had to maintain a stable performance, with no visible trend in choice proportion over the last three sessions.

Table 5

Number of Trials per Type (Short, Long, or Probes) and Corresponding Base-rates and Payoffs for Experiment 1B During Training and Test Phases of Each Condition

Condition	Phase	Number of Trials			Base-rate		
		S	L	Probe	*s*	*l*	Δ
LB$_{(0.1-0.9)}$	Training	12	108	-	.10	.90	-.80
	Test	6	54	36			
LB$_{(0.2-0.8)}$	Training	24	96	-	.20	.80	-.60
	Test	12	48	36			
NB$_{(0.5-0.5)}$	Training	60	60	-	.50	.50	.00
	Test	36	36	36			
SB$_{(0.8-0.2)}$	Training	96	24	-	.80	.20	+.60
	Test	48	12	36			
SB$_{(0.9-0.1)}$	Training	108	12	-	.90	.10	+.80
	Test	54	6	36			

Results and Discussion

Figure 20 shows the average psychometric functions per condition and their corresponding best-fitting cumulative Gaussian functions (Table D2, Appendix D, lists the best-fitting parameters) for each test session. Performance at the anchors remained accurate during testing, with only a small decrease for L in condition LB$_{(0.9-0.1)}$. As the signal duration increased, the pigeons showed a smooth transition from a strong preference for “short” to an almost absolute preference for “long.” Overall, in conditions with the base-rate contingencies favoring the L sample, the psychometric functions shifted to the left, whereas when they favored S, they shifted to the right. Additionally, SB conditions seem to affect p(“long”) mostly for longer durations and LB mostly for shorter durations.

A repeated measures ANOVA ran on data from Test 1 yielded significant effects of condition, $F(4, 24) = 3.13$, $p = .033$, $\eta_p^2 = .0.342$, and of sample duration, $F(4, 24) = 234.42$, $p < .001$, $\eta_p^2 = .975$, but not of their interaction, $F(16, 96) = 1.23$, $p = .257$, $\eta_p^2 = .171$. Test 2 also showed significant effects of condition, $F(4, 24) = 3.29$, $p = .028$, $\eta_p^2 = .354$, and sample duration, $F(4, 24) = 157.95$, $p < .001$, $\eta_p^2 = .963$, but not of their interaction, $F(16, 96) = 0.69$, $p = .800$, $\eta_p^2 = .103$. In Test 3, however, conditions cannot be differentiated, $F(4, 24) = 0.78$, $p = .552$, $\eta_p^2 = .114$. Similarly to Experiment 1A, extended exposure to testing brought the functions closer together, albeit to a lesser degree. Although we kept base-rate differential equal from training to testing in Experiment 1B, it is possible that reinforcment of probe responses, which were presented equally throughout the experiment, caused this reduction in the effect of each condition. Thus, only parameters for Test 1 were analyzed.

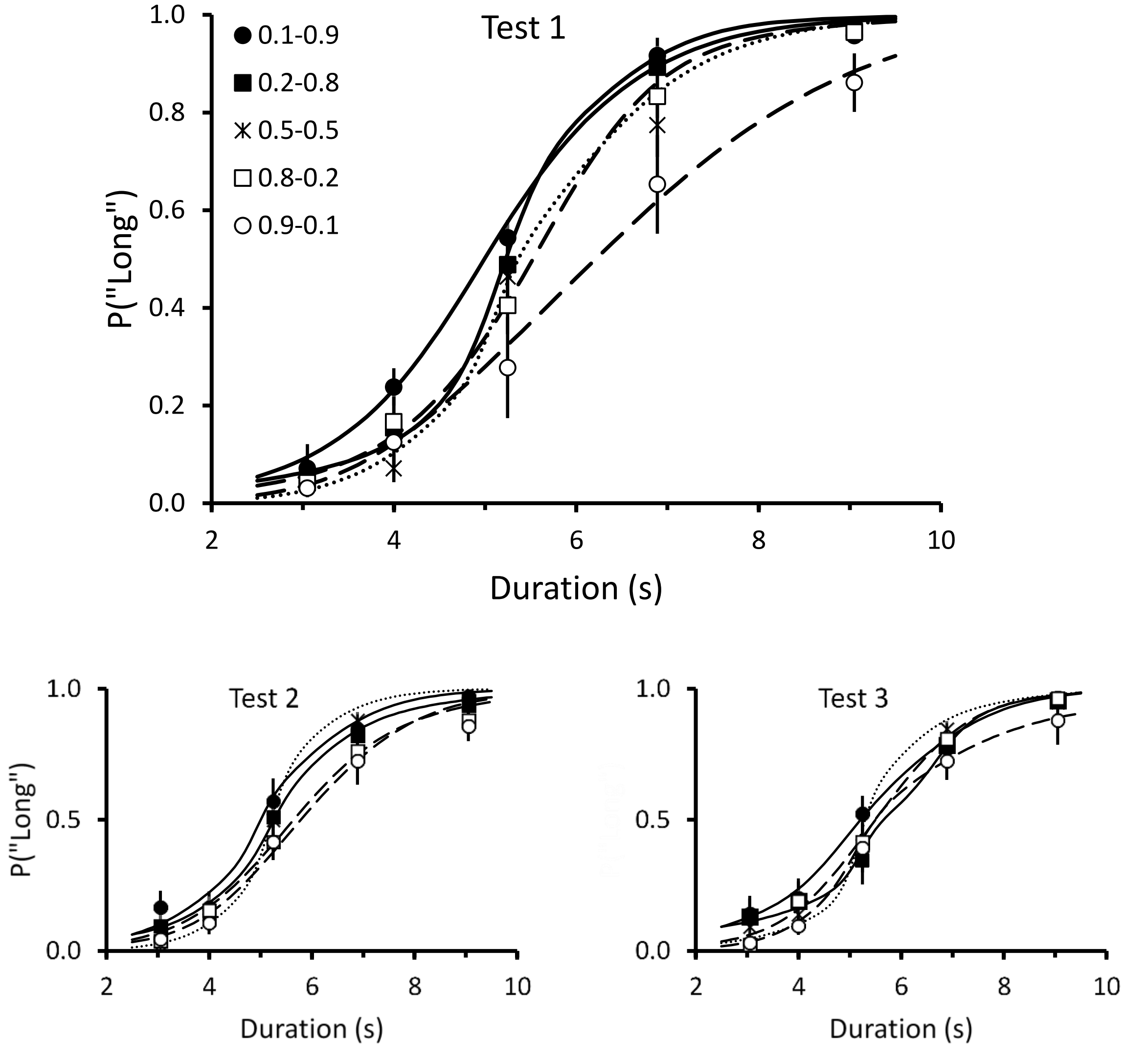

Figure 20. Proportion of "long" responses (*M* ± *SEM*) for each condition: $LB_{(0.1\text{-}0.9)}$ (solid circles), $LB_{(0.2\text{-}0.8)}$ (solid squares), $NB_{(0.5\text{-}0.5)}$ (asterisks), $SB_{(0.8\text{-}0.2)}$ (empty squares) and $SB_{(0.9\text{-}0.1)}$ (empty circles), and corresponding curves with averged parameters from individually fitted cumulative Gaussians (solid lines for LB, dashed lines for SB, dotted line for NB), in Experiment 1B. Top panel shows first test session, bottom panel shows second (left) and third (right) test sessions. NB = No-Bias, LB = Long-Bias, SB = Short-Bias.

The location parameters from the individual cumulative Gaussian fits corroborated the shifts found in Test 1. As the top panel of Figure 21 shows, the PSE varied with Δ: It was smaller in conditions with positive Δ and larger in conditions with negative values. A repeated measures ANOVA yielded significant differences in μ across conditions, $F(4, 24) = 3.14$, $p = .033$, $\eta_p^2 = .344$. Although visual inspection of the averaged psychometric functions may suggest changes in sensitivity, the scale parameters from the cumulative Gaussian fits, displayed in the bottom panel of Figure 21, revealed no consistent changes, $F(4, 24) = 0.56$, $p = .694$, $\eta_p^2 = .085$. To summarize, as in Experiment 1A, the effect of differential payoff was expressed as horizontal shifts in the psychometric functions and the consequent change in PSE, but not as changes in sensitivity.

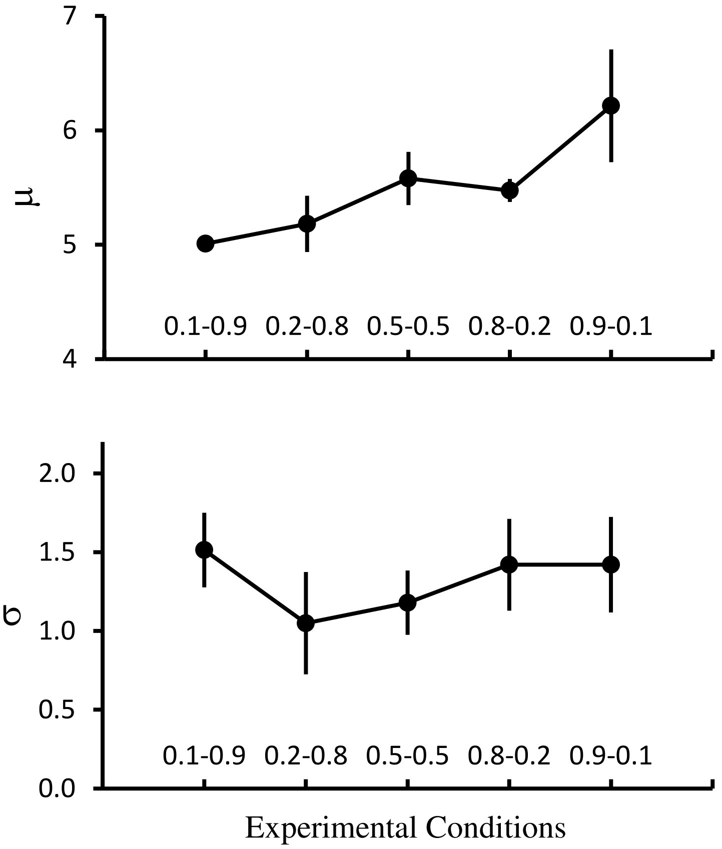

Figure 21. Parameters per condition (*M* ± *SEM*) from individual cumulative Gaussian fits: μ (top), σ (bottom) of Experiment 1B.

Experiments 1A and 1B extended the base-rate manipulation investigated in previous studies (Akdoğan & Balcı, 2016a; Balcı et al., 2009; Çoşkun et al., 2015; Jozefowiez et al., 2014). These studies showed that higher base-rates increase response bias towards the higher-rate / more frequent key, while sensitivity to time, when assessed, remains relatively unaffected. Although our studies differed in several procedural aspects, the direction of the shifts of the psychometric functions covaried systematically with Δ.

Experiment 2

Analyzing behavior during the sample can help us understand the timing processes taking place during the sample as well as how they relate to choice when base-rate differs for S and L samples. To simplify, we used only two Δ values, −0.6 and +0.6, which remained in effect during Base-rate Tests. This experiment aimed to generalize and expand the findings from Experiment 1.

Method

Subjects. Six pigeons were maintained at 85% of their free-feeding body weights. All had previous experience with standard operant chambers, in experiments related to choice in concurrent-chains schedules. Housing conditions remained as in Experiment 1.

Apparatus. The long operant chamber used in this experiment has been previously described and is pictured in Chapter II (Figure 10). Overall dimensions were 96 x 31 x 33 cm (length x depth x height). Each aluminum side wall and the back was equipped with one houselight (28-V, 0.1-A), three circular response keys, and a feeder opening that lit (with a 28-V, 0.04-A bulb) when activated. Houselights were horizontally centered on each wall, 1.5 cm from the ceiling. Keys were 2.5 cm in diameter, separated by 8 cm center-to-center, and 24 cm above the floor. Feeder openings (6 cm wide x 5 cm high) were horizontally centered on each wall and 9 cm above the floor.

The floor consisted of three rectangular metal aluminum panels, placed side by side, each with a fulcrum in the middle and two switches underneath, one at each end. When the bird moved to one segment, it tilted the panel and activated the switch at that location. Thus, the chamber was divided into 6 locations (left and right sides of each of the three panels, numbered from 1 (leftmost) to 6 (rightmost). A computer controlled all experimental events and recorded the data using ABET II® software (Lafayette Instruments).

Procedure. Initially, pigeons were trained to eat from all three feeders, and to peck the left key of the left panel, the center key of the center panel and the right key of the right panel (hereafter referred to as the left key, center key, and right key, respectively). We then shaped them by successive approximations to step on location 1 or 6 to turn on the left or right keys, respectively, after pecking a green center key. This procedure ensured that pigeons could only choose a key when standing at the end locations, thus using the full extension of the chamber. Each training step was in effect for two sessions: step 1: locations 3 and 4; step 2: locations 2 and 5; and step 3: locations 1 and 6.

Pigeons were trained in a bisection task in all subsequent phases. Trials followed the same general structure: Following a 20-second ITI with only the center houselight on, the green center key turned on. A single peck switched the key color to red for either 3 (S) or 12 s (L) and turned on both the left and right houselights. Once the signal elapsed and the center key and the side houselights turned off, the pigeon could illuminate in a red hue the left or right keys by stepping on Locations 1 or 6, respectively. Trials ended when a response was recorded on an illuminated side key. The corresponding feeder delivered grain, given the response was correct. For three pigeons, pecking the left key was reinforced in S trials, while pecking the right key was not. The key assignment was the opposite on long trials. For the remaining pigeons, the reverse assignment was in effect.

Discrimination Training. Initially, all trials (minimum of 40 S, 40 L, randomly intermixed) were reinforced provided the choice was correct. Incorrect responses led to the repetition of the trial (i.e., a correction procedure was in effect). During the first session, one error led to a forced trial, in which only the correct comparison key could be turned on after the sample. During the second session, forced trials occurred only after two consecutive errors. From the third session onward, three consecutive errors started a forced trial.

The learning criterion was 80% correct per sample, excluding correction trials. When the birds met the learning criterion for three consecutive sessions and had completed a minimum of 15 sessions, the proportion of reinforcement after a correct choice in all trials was reduced from 1.0 to .75 in a single step. The correction procedure remained in effect for the reinforced trials; incorrect responses in extinction trials did not lead to the repetition of the trial. Pecks on the center key were reinforced with food with a probability of .1 to maintain the pecking response for the remaining of the experiment. This phase remained in effect until the subjects met the learning criterion for five consecutive sessions.

In all subsequent training and test phases, we removed the correction procedure, and correct key presses were reinforced with a probability of .5 so that relative and overall rates remained approximately constant throughout the experiment.

Base-rate Training. Each bird went through all conditions, which differed only in base-rate (i.e., the proportion of S and L trials): No-Bias (NB), Short-Bias (SB), and Long-Bias (LB). Table 6 shows the base-rate and payoffs for each condition. In the No-Bias conditions, 50% of the trials presented S samples and 50% L samples. All pigeons started with No-Bias, NB, and feeder durations were adjusted within the first five sessions so that each pigeon was kept at 85% of its free-feeding weight throughout the experiment (range: 1.6 – 2.0 s). Subsequent NB conditions occurred after SB and LB to reduce possible carry-over effects between conditions with unequal base-rates.

Table 6

Number of Trials per Type (Short, Long, or Probes), Corresponding Base-rates, and Overall Payoffs for Experiment 2 During Training and Test Phases

Condition	Phase	Number of Trials			Base-rate			Overall Payoff
		S	L	Probe	*s*	*l*	Δ	
	Discrimination Training	40	40	-	.50	.50	.00	1.00
		40	40	-	.50	.50	.00	.75
$LB_{(0.2\text{-}0.8)}$	Training	16	64	-	.20	.80	-.60	.50
	Test	16	64	16	.20	.80	-.60	.42
$NB_{(0.5\text{-}0.5)}$	Training	40	40	-	.50	.50	.00	.50
	Test	40	40	16	.50	.50	.00	.42
$SB_{(0.8\text{-}0.2)}$	Training	64	16	-	.80	.20	+.60	.50
	Test	64	16	16	.80	.20	+.60	.42

Note. LB = long bias, NB = no bias, SB = short bias.

Condition LB had 80% L trials (64 trials), whereas only 20% of the trials (16 trials) presented the S sample. Reverse probabilities were in effect in SB. Trials were selected without replacement from a 10-item list. For half of the pigeons, the first bias condition was SB followed by LB (P737, PG18, and P960); we reversed the order for the other half (PG39, P1727, and P456). The training phase for each condition was in effect for at least ten sessions. To continue to the test phase, animals had to meet the learning criterion for three consecutive sessions.

Base-rate Test. Testing occurred immediately after each condition, and S and L samples were presented in the same proportion as in their preceding Base-rate Training phase. Besides the 80 regular training trials, 18 non-reinforced probe trials were added with the new durations: 1.5, 4.2, 6, 8.5, 17, and 24 s (three trials per sample). The shortest (1.5 s) probe was half of S. All other samples approximate a geometric series with ratio 1.4. This phase ran for six sessions.

Analysis of motion patterns. For simplicity, we assume that, for all subjects, the shortest location is 1 and the longest is 6. Let $\lambda(t)$ denote the pigeon's location at time t, with

$\lambda(t) = 1, 2,\ldots,6$, and $0 \leq t \leq$ sample, with t measured in 0.5-s slices. We define Arrival Time at the *short* side (AT_S) of the chamber as the time since sample onset at which $\lambda(t)$ reached its minimum value. Departure times (DT) were defined only on trials the pigeon moved to the *long* side of the chamber and were obtained from when the animals stepped on the second farthest location from the *long* side. That is, if the animal arrived at the farthest location (i.e., $\lambda(AT_S) = 1$), we considered the departure time as the slice it moved to location 2. Residence time equaled DT – AT_S. Arrival Time at the *long* side (AT_L) is the t at which $\lambda(t) = 6$ for the first time. We classified the motion patterns as follows: The pigeon moved towards the (1) *short* side, and stayed there until the end of the sample – pattern *S*; (2) *short* side first, then to the center of the chamber, and finally returned to the *short* side – pattern *SS*; (3) *short* side first and then to the *long* side – pattern *SL*, or; (4) *long* side and stayed there – pattern *L*.

Results and Discussion

In the temporal Discrimination Training phase, five pigeons met the learning criterion within two to five sessions, and one subject (PG39) required 12 sessions to meet the criterion. Figure 22 shows a representative example of motion patterns in this phase (PG18) for L trials. The solid line represents the median location through time, and the lower and upper dotted lines represent the first and third quartiles, respectively. The top and the bottom-left graphs show acquisition of the temporal discrimination (100% reinforcement) in three moments: first session, last session before reaching the learning criterion, and final session. As training progressed, pigeons learned to approach the *short* side, wait, and move to the *long* side, where they remained until the end of the trial (pattern *SL*). Variability of motion patterns decreased across sessions for all birds.

In the last session before reducing the proportion of reinforcement, arrival at the *short* side (AT_S) was on average 2.79 s into the sample (*SD* = 1.42 s), residence was 3.19 s (1.41 s), and DT averaged 5.59 s (1.38 s). AT_L was 8.76 s (1.83 s). Pattern *SL* accounted for 93% of all long trials (averaged across subjects, except PG39). This pattern is the same as shown in previous experiments using a similar apparatus (Cambraia et al., 2019; Machado & Keen, 2003). By moving this way, pigeons make sure they will be at the corresponding baited key at trial offset – the moment of choice –, i.e. at the *short* side after the short interval and *long* after the long interval. However, one animal (PG39) had a different strategy: it remained at the center before moving to the *long* side (pattern *L*). Although this pattern does not guarantee that the deprived animal will obtain food as fast as possible on the S trials, it can also be considered adaptive in the sense that it saved energy on the L trials by not move all the way to the *short* side at trial onset.

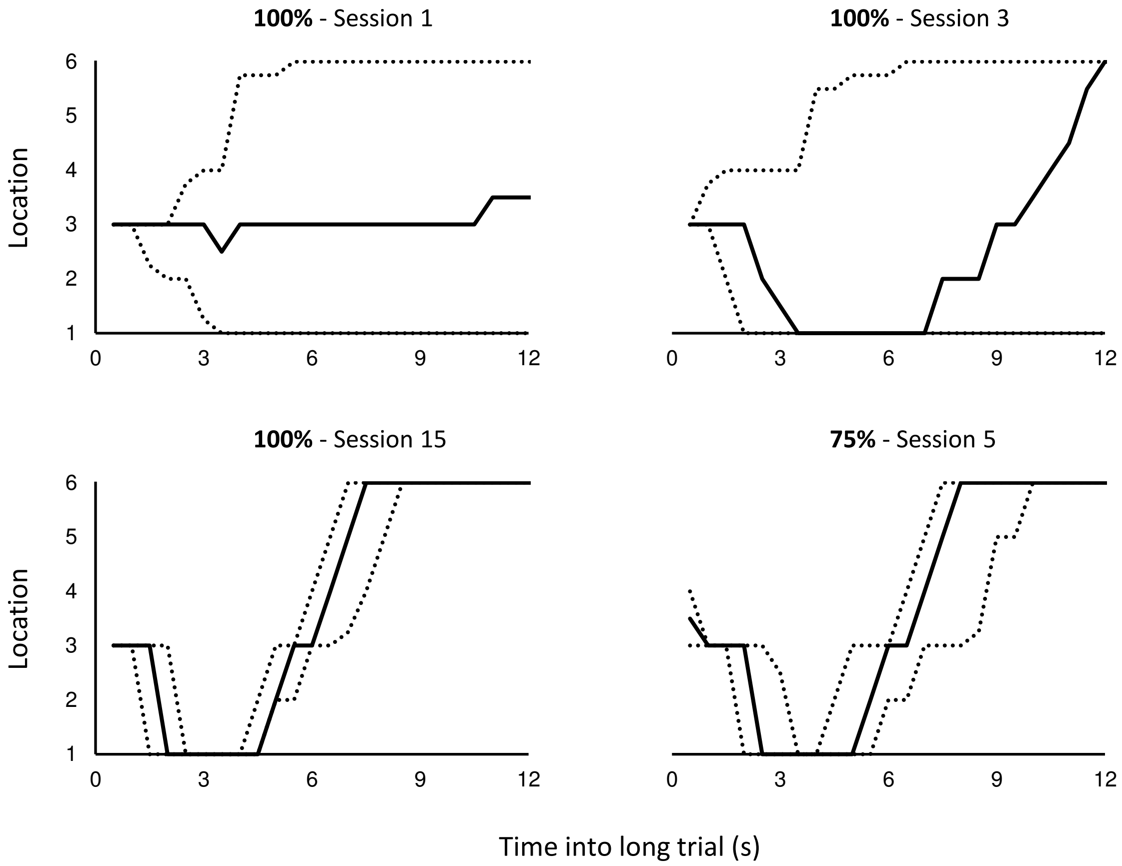

Figure 22. Movement patterns on L trials on Temporal Discrimination training (subject PG18). Top-left: First session with 100% reinforcement. Top-right: Last session before reaching learning criterion (Session 3). Bottom-left: Last session with 100% reinforcement (Session 15). Bottom-right: Last session with 75% reinforcement (Session 5). The lines are, from top to bottom, the third (dotted line), second (solid line), and first (dotted line) quartiles of the birds' location during the long trials. Training signals were 3- and 12-s long.

Although the representative pigeon shows a slight increase in variability when reinforcement decreased to 75% (Figure 22, bottom-right), this is not consistent across birds, i.e., some showed no difference, some showed a decrease. This data replicates Cambraia et al. (2019, Experiment 2). A paired sample t-test confirmed there were no significant differences between the last sessions with 100% and 75% reinforcement for parameters AT_S, DT, or AT_L (all *p*s > .12).

The average psychometric functions per condition, and their individually fitted Gaussian functions (individual parameters in Table E1, Appendix E), are shown in Figure 23 (top panel), as well as the location (μ, bottom left) and scale parameters of the fits (σ, bottom right). The functions are typical sigmoidals, ranging from close to 0 at the shortest durations, to close to 1 at the longest durations. A repeated measures ANOVA confirmed effects of duration, $F(7, 35) = 123.17$, $p < .001$, $\eta_p^2 = .961$. Responding outside the anchors was categorical, with 1.5 s classified primarily as "short" and 17 and 24 s as "long". There was a significant effect of condition, $F(2, 10) = 27.00$, $p < .001$, $\eta_p^2 = .844$, which is consistent with Experiment 1 as well as previous experiments. The interaction between condition and duration was also significant, $F(14, 70) = 2.26$, $p = .013$, $\eta_p^2 = .311$.

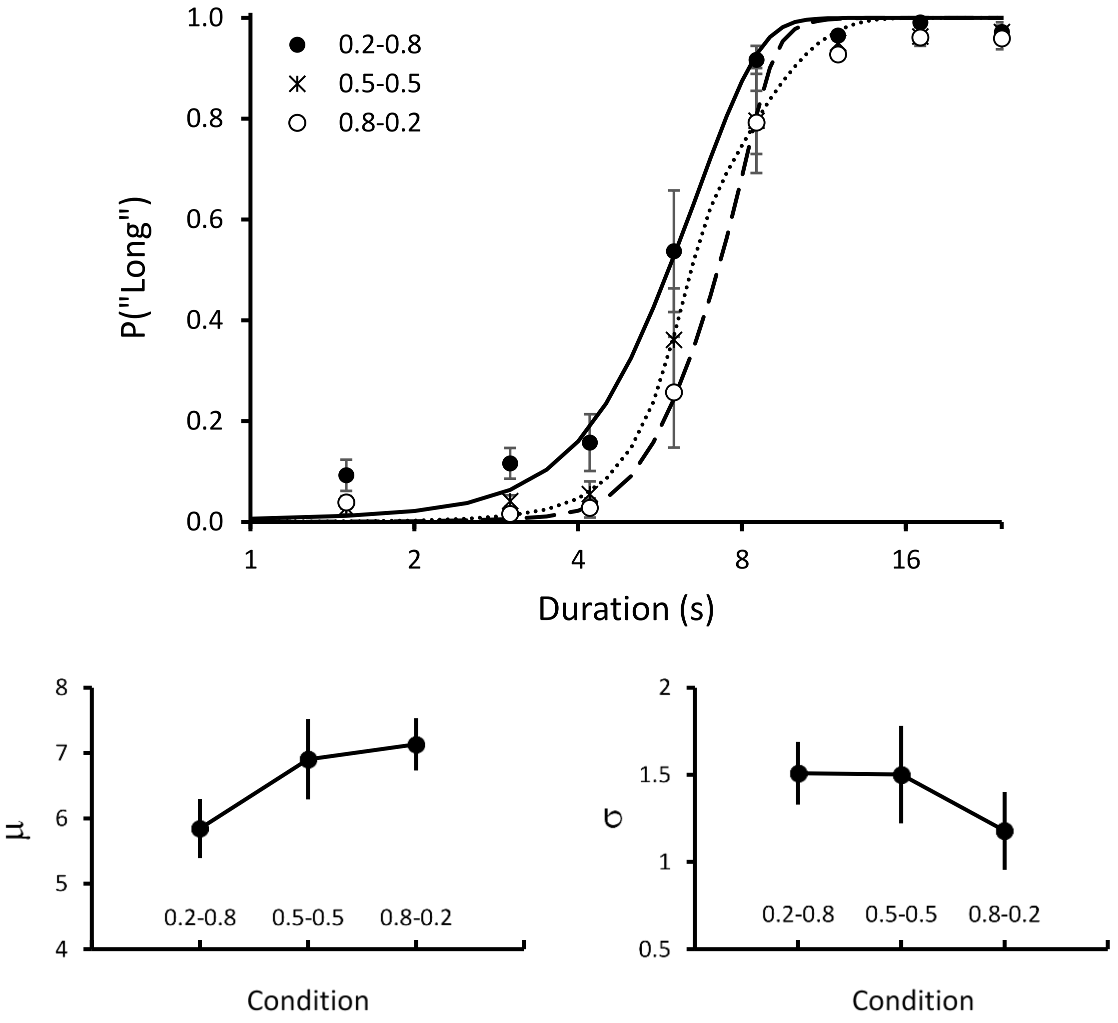

Figure 23. Top: Proportion of "long" responses (*M* ± *SEM*) for each condition: LB$_{(0.2\text{-}0.8)}$ (solid circles), NB$_{(0.5\text{-}0.5)}$ (asterisks), SB$_{(0.8\text{-}0.2)}$ (empty circles), and corresponding curves with average of individually fitted cumulative Gaussians (solid line for LB, dashed line for SB, dotted line for NB), in Experiment 2. Bottom: Location (μ; left) and scale (σ; right) parameters of the fits. NB = No-Bias, LB = Long-Bias, SB = Short-Bias.

The PSE (μ) averaged 6.91 (*SEM* = 0.61) at baseline, which is above the geometric mean of the anchors (6 s) and below the arithmetic mean (7.5 s), similarly to Experiment 1A. Overall differences in conditions reached statistical significance, $F(2, 10) = 12.42$, $p = .00$, $\eta_p^2 = .71$. Together with the overall shifts in the psychometric functions, this indicates base-rate biased responding. The σ parameter did not differ significantly across conditions, $F(2, 10) = 0.39$, $p = .69$, $\eta_p^2 = .07$. Thus, while there is no evidence of the base-rate differential affecting sensitivity, pigeons were biased towards responding on the key associated with the highest probability of sample occurrence, as in Experiment 1.

Figure 24 (top panel) shows the empirical cumulative distribution function of departure times (individual parameters in Table E2, Appendix E). The distribution for condition $\mathrm{LB}_{(0.2\text{-}0.8)}$ shows a small leftward shift at $p = 0.5$, compared to $\mathrm{SB}_{(0.8\text{-}0.2)}$. More conspicuous, however, is the upward shift early in time. It indicates that presenting more L trials increased the likelihood of the animals departing to the long side very early into the trials. In fact, in condition $\mathrm{LB}_{(0.2\text{-}0.8)}$, they went straight to the long side (pattern *L*) on 19% of the long trials, on average (*SEM* = 0.06); compared to 10% (± 0.06) in $\mathrm{SB}_{(0.8\text{-}0.2)}$ and 5% (± 0.01) in $\mathrm{NB}_{(0.5\text{-}0.5)}$.

Machado and Keen (2003) reported that the distribution of departure times was equivalent to the psychometric function because it matched the proportion of "long" choices for a range of sample durations. In other words, time of departure from the *short* side during the sample predicted key choice at the end of the sample, which the authors named "short/no-short hypothesis." However, Cambraia et al. (2019) observed that, in conditions with unequal reinforcement probabilities, a) the birds did not always go to the shortest side of the chamber, b) departure time was no longer the best predictor of key choice for intermediate durations, and c) the interaction between payoffs and location of the subject at sample offset was a good predictor of "long." In other words, the closer to the *long* side at the time of choice, the higher the p("long"), with animals more likely to be located closer to *long* at sample offset when that side had higher payoffs.

In the current experiment we saw, again, a dissociation between the distribution of departure times and key choice for intermediate durations (Figure 24, bottom panel), for each experimental condition. This means that, sometimes, although the pigeons had already departed for the long side, they returned to peck at the *short* side of the chamber (pattern *SS*). For the 6-s sample, this occurred on average on 19% (±0.08) of the trials in LB, 41% (±0.12) of the trials in NB, and 33% (±0.09) of the trials in SB. Interestingly, LB had the best match compared to NB and SB. In LB, the animals were less likely to return (*SS* pattern) choose "short" because they were less likely to be at the *short* side at sample offset, as depicted in Figure 9. Cambraia et al. (2019), on the other hand, found that the distribution in NB fit well the proportion of "long", while bias conditions, LB and SB, presented large a mismatch, especially for intermediate probes. This effect was attributed to a reduction in temporal control in payoff biasing conditions.

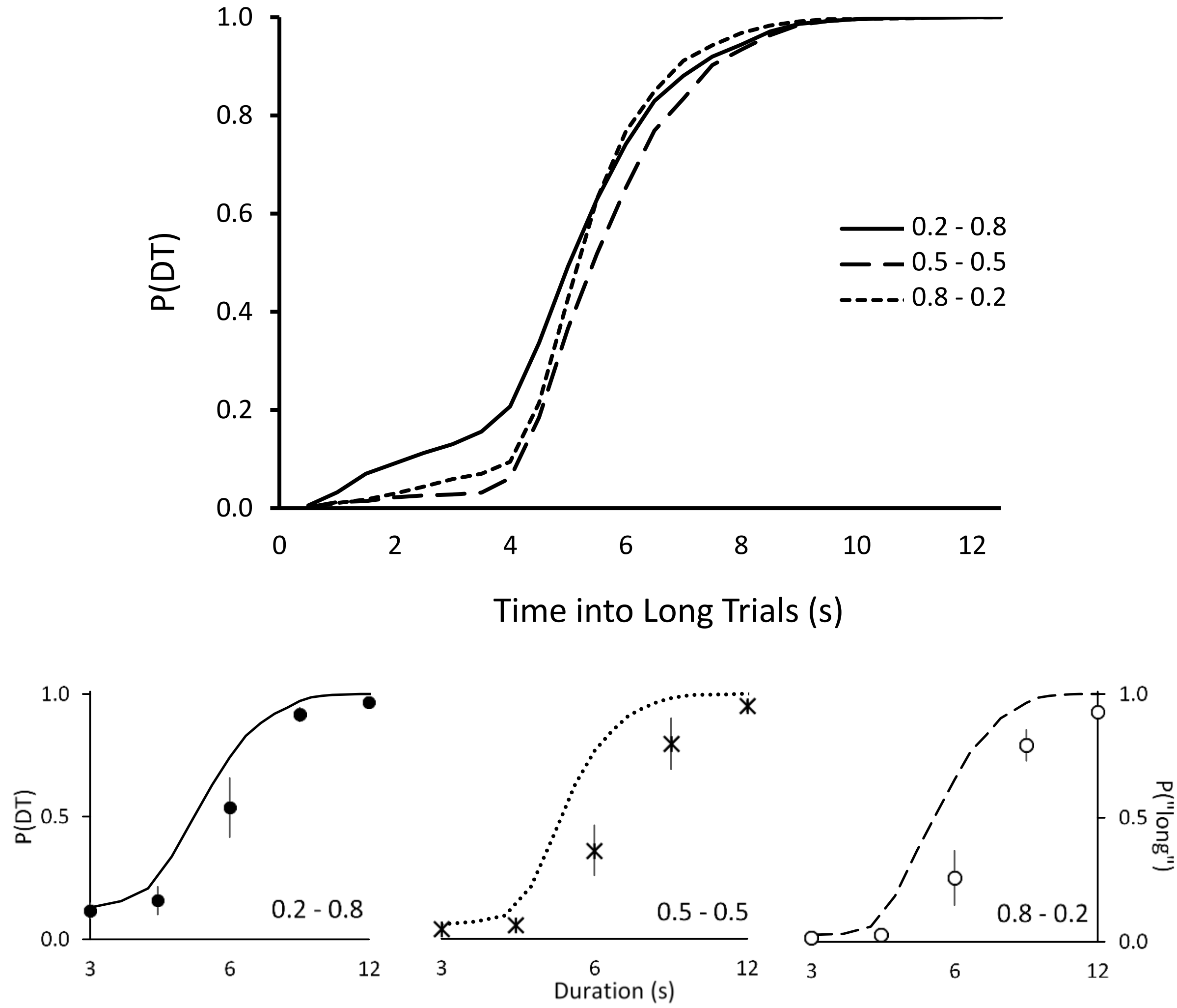

Figure 24. Top: Averaged empirical cumulative distribution function of departure times (ECDF of DT) in L samples for conditions $\text{LB}_{(0.2\text{-}0.8)}$ (solid line), $\text{NB}_{(0.5\text{-}0.5)}$ (dotted line), and $\text{SB}_{(0.8\text{-}0.2)}$ (dashed line). Bottom: ECDF of DT plotted against proportion of "long" for conditions $\text{LB}_{(0.2\text{-}0.8)}$ (left), $\text{NB}_{(0.5\text{-}0.5)}$ (center), and $\text{SB}_{(0.8\text{-}0.2)}$ (right). NB = No-Bias, LB = Long-Bias, SB = Short-Bias.

Figure 25 indicates, in a grayscale gradient, the proportion of trials the animals were at each location (λ) for different slices of time (t) in L samples, i.e., p(λ|t). The darker the shade, the greater the value of p. Let us examine condition NB (top): The darkest rectangles move from the center ($\lambda = 3, 4$) at trial onset, to the *short* side ($\lambda = 1$), and then to the *long* side ($\lambda = 6$), staying mostly at location 1 when t = 4.2 s and location 6 when t = 12 s. Note that this also indicates where the birds are most likely to be at probe offset – somewhere between the *short* an the *long* side, especially at 6 s. These findings agree with the general motion patterns revealed by the median motion curves in Figure 22 (bottom panel) but is more informative considering the mixture of motion patterns, as specified next.

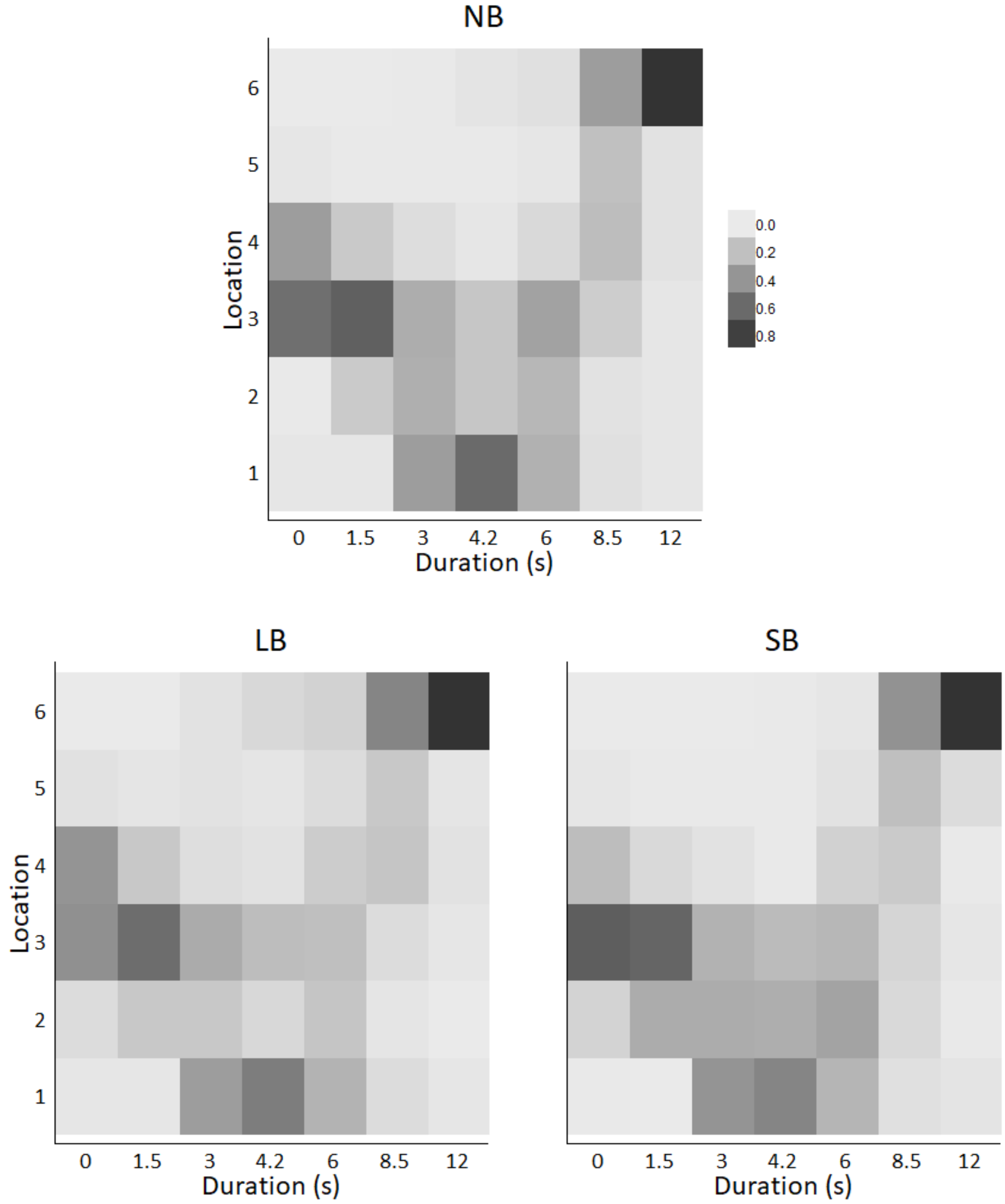

Figure 25. Average proportion of trials birds were on each location at different time points of the 12-s sample, for conditions $NB_{(0.5-0.5)}$ (top), $LB_{(0.2-0.8)}$ (bottom-left), and $SB_{(0.8-0.2)}$ (bottom-right). NB = No-Bias, LB = Long-Bias, SB = Short-Bias.

Conditions LB (bottom left) and SB (bottom right) still show the predominance of the *SL* pattern, but with greater spreading of shade across locations. Comparing the top half ($4 \leq \lambda \leq 6$), LB is darker, consistent with the earlier departure times and the higher occurrence of *L* patterns. SB, on the other hand, is darker at the bottom half ($1 \leq \lambda \leq 3$), consistent with the later departure times and higher occurrence of *SS* patterns. These are behavioral effects of the base-rate manipulation that can be seen throughout the sample intervals and complement the psychometric function obtained from responding at the end of the sample.

Figure 26 shows the pooled proportion of "long" choices for all intermediate probes, given that the animals were at each location at sample offset (refer to Appendix F for number of "long"/frequency at location, per sample). Overall, it shows that the closer to the *long* side, the higher the p("long") — conversely, the closer to the *short* side, the higher the probability of choosing "short," including trials the birds had already departed from short. This effect interacts with the experimental condition because when biased for long, birds are more likely to choose "long" overall, when compared to the other conditions.

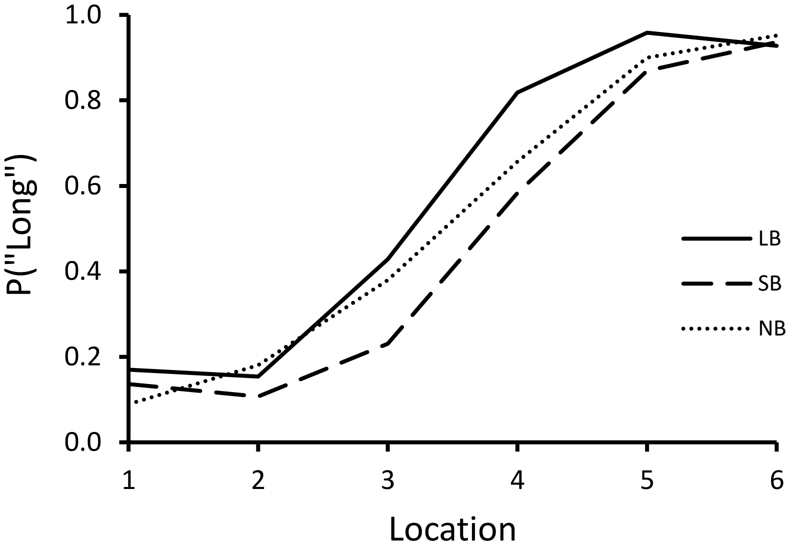

Figure 26. Proportion of "long" given location at sample offset, pooled.

In conclusion, this experiment replicated findings from Experiment 1 by showing that differential base-rates affect response bias but not sensitivity to timed intervals. Moreover, location data extended results from Experiment 1 by producing a better understanding of the timing processes during the samples. Interestengly, comparing choice and location data showed a mixture of motion patterns, especially for the intermediate probes, which interacted with experimental condition. For instance, increasing the base-rate of L trials led to a higher likelihood of the animals moving to the *long* side very early into the trials, often directly from the center of the chamber (pattern *L*). Also, the distribution of departure times was better matched by p("long") in condition LB because the animals were most likely oriented towards the *long* side of the chamber and thus the *SS* pattern was less likely to occur. Thus, location of the subjects in time is a good predictor of choice at sample offset, with condition affecting location.

General Discussion

The present study investigated the effects of differential base-rates of short (S) and long (L) trials in a bisection task. In Experiments 1A and 1B, pigeons went through a typical bisection task, learning a duration-key color mapping (e.g., S—red, L—green), before being exposed to five conditions with differential base-rates. Experiment 2 extended the previous studies to a long operant chamber, with response keys far apart and sensitive floor panels that recorded the pigeon's location throughout trials. In that chamber, the pigeons learned a time-place mapping (e.g., S—left, L—right). To measure the effects of varying the base-rate differential, we computed psychometric functions based on choice proportion and estimated their location and scale parameters, measures of response bias and temporal sensitivity, respectively. In Experiment 2, we also compared the pigeons' motion patterns during the sample to choice after sample offset.

Results showed that a higher proportion of L-sample trials produced leftward shifts in psychometric functions, decreasing the PSE. Conversely, a higher proportion of S-sample trials produced a rightward shift, increasing the PSE. This was consistent throughout our study, despite the different testing strategies. Altogether, the experiments showed differences in animals' preference for "short" or "long" that were consistent with the relative base-rates of each conditional stimulus, a bias effect. There were no systematic changes in sensitivity.

These results extend the generality of previous findings from studies manipulating differential base-rates in the temporal bisection task (Akdoğan & Balcı, 2016a; Jozefowiez et al., 2014) and switch task (Balcı et al., 2009), to pigeons and intermittent reinforcement. They are also comparable to those found for differential payoffs associated with "short" and "long" responses in a bisection task (Cambraia et al., 2019). Although the payoff differential remained constant (zero) throughout our set of studies, when manipulating base-rates, animals obtained a higher proportion of reinforcers for producing one response over the other. Thus, it could still be possible that the subjects are affected by the "short"/"long" payoff ratio and not exclusively by base-rates. Showing that animals respond similarly to differential base-rates when payoffs are intermittent paves the way to study whether maintaining equal payoffs ratios, rather than a null differential, would affect behavior under unequal base-rates of short and long samples.

Associative timing models such as Learning-to-Time (LeT; Machado, 1997a; Machado et al., 2009) and the Behavioral Economic Model (BEM; Jozefowiez et al., 2009) predict a bias effect for differential base-rates. The Scalar Expectancy Theory (SET; Gibbon, 1977, 1981) does not predict biased performance without further assumptions. Jozefowiez et al. (2014) compared BEM to a modified SET and found that the SET simulation for differential base-rates produces very large shifts between biasing conditions, while BEM produces much more modest shifts. Our results, together with Akdoğan & Balcı (2016a), confirm small shifts in the temporal bisection task with pigeons and mice, respectively.

However, in the current state, none of these models can account for all the motion data from Experiment 2. We observed similar shifts on the trial-by-trial PSEs, i.e., birds departed earlier when presented with more long samples; however, the distribution of departure times shifted to a lesser degree than the psychometric function. The most striking effect was found very early into the trials: pigeons were more likely to go straight to the *long* side of the chamber soon after trial onset than when there were more short trials. Thus, although the distribution of departure times is also sensitive to differences in relative payoff, such early departures indicate that the animals were not timing on some trials but instead were under control of the most frequent stimulus, which strengthened the association between pecking and the “long” key. Timing models, such as that described by Daniels et al. (2015), which consider the occurrence of non-timing states are best equipped to predict behavior under differential base-rates.

Experiment 2 also brought to light the relationship between motion patterns during the trial and final choice in a bisection task. Although the distribution of departure times was affected by experimental condition, it did not predict choice accurately; instead, the location of the bird at sample offset was the best predictor of choice – the closer to the *long* side, the higher the probability of choosing “long.” The distribution of departure times in condition LB seemed to be the best predictor compared to NB and SB. This measure does not suffer as much in LB because the animals quickly move to the long side of the chamber, and do not return (pattern *SS*). In the other conditions, they are closer to the *short* side on more trials, increasing the likelihood of choosing “short”, even after departing. Timing models that consider competition for behavioral control by different stimulus dimensions may help explain the mechanisms behind the disassociation of motion and choice in the time-place bisection task (e.g., Cowie et al., 2014; Daniels, Fox, et al., 2015).

To conclude, the present study confirmed that control of temporal behavior depends on differences in relative base-rates between the short and long sample stimuli in a bisection task. The unequal presentation of short and long samples in a session biased responding as measured by key preference and motion, while we observed no significant changes in sensitivity. The mechanisms behind these effects could be better explained by models of timing that consider not only the role of time on behavior, but also of other stimulus dimensions, and the occurrence of non-temporally-controlled behaviors.

CHAPTER IV

DIFFERENTIAL PAYOFF EFFECTS ON HUMANS

I would like to thank Mehdi Bugallo for help planning and collecting data for Experiment 1.

Abstract

We investigated how differential payoffs affect the temporal discrimination of humans. In a temporal bisection task, participants learned to make one response after a short sample and another after a long sample. When presented with a range of intermediate samples, the proportion of responses fitted well a Gaussian-like distribution function characterized by a location (bias), a scale (sensitivity) parameter, and two asymptote (discrimination) parameters. In Experiment 1, when one response yielded more reinforcers than the other, parameters were unaltered, but overall responses increased for the response producing higher payoffs. In Experiment 2, we used a video game to track motion during the sample and participants learned to approach the “short” response location at sample onset and remain there before departing to the “long” location on long trials. Departure times were shorter when “long” choices produced higher payoffs than “short” and matched well the shifted psychometric functions. However, on some trials, subjects were biased for short, returning to the short side after having departed towards long. Evidence was found for effects of differential payoffs on response bias, but discrimination and sensitivity did not change consistently. These results favor a behavioral account of timing processes.

Reinforcement is widely considered to play a central role in timing. From the viewpoint of the leading cognitivist model of timing, Scalar Expectancy Theory (SET; Church & Gibbon, 1982; Gibbon, 1977, 1991), reinforcement causes the formation of temporal memories for cued intervals. Alternatively, in the perspective of behavioral models of timing such as the Learning-to-Time model (LeT; Machado, 1997b; Machado et al., 2009), reinforcement is viewed as the element which strengthens the associations between time-dependent behavioral events and responses, causing responding to adapt to temporal regularities in the environment.

Diverse alterations of the reinforcement regime have been shown to produce modifications of temporally-controlled behavior. Studies have reduced overall reinforcement (e.g., Bizo & White, 1994b, 1994a; Galtress & Kirkpatrick, 2009; Killeen & Fetterman, 1988; Morgan et al., 1993), changed the relative reinforcement between shorter and longer durations (Bizo & White, 1995; Cambraia et al., 2019; Daniels, Fox, et al., 2015; Galtress & Kirkpatrick, 2010; Guilhardi et al., 2007; Machado & Guilhardi, 2000; Stubbs, 1976), and manipulated deprivation levels by feeding the animals prior to the task (e.g., Daniels & Sanabria, 2017; Grace & Nevin, 2000),

Typically, the psychometric function plotting retrospective judgments about sample durations (e.g., the probability of long) as a function of stimulus duration is sigmoid in shape (Staddon et al., 1991). For many tasks, such as the temporal bisection (Church & Deluty, 1977), this function is well described by a cumulative Gaussian distribution with a mean parameter, μ, representing the subjective middle point between the two extreme durations, often referred to as the point of subjective equality (PSE), and the standard deviation or scale parameter, σ, indicating sensitivity to the passage of time (Gibbon, 1981).

Changes in the PSE tend to be the more robust effect of differential reinforcement, especially in the Free-operant Psychophysical Procedure (FOPP; Stubbs, 1980). This indicates a horizontal shift of response functions, a response bias effect (Blough, 1996). For example, Bizo and White (1995) varied the reinforcement rates in the two trial halves of a FOPP and found that pigeons biased their choices toward the key associated with the richer schedule, shifting the functions rightward when the most reinforcers were available during the first half and leftward when the second half was richer.

The temporal bisection task, one of the most common procedures in the study of human and non-human timing, has produced similar (Stubbs, 1976), but not always consistent

(Galtress & Kirkpatrick, 2010) bias effects. This is a discrete-trial task that requires classification of stimuli of different durations as “short” or “long”. Although the vast majority of reports are on the effects of reinforcement on timing with non-human animals, one study has investigated the effects of differential payoffs on humans.

Akdoğan and Balcı (2016b) invited 20 participants to perform a bisection task in three separate sessions. In each session, participants went through a training phase, in which they learned to respond in relation to two samples: 1 s (short; S) and 1.5 s (long; L). During testing, non-reinforced intermediate samples were also presented, and points for correct responses were either higher for S-trials (Short-Bias), for L-trials (Long-Bias), or were equal for S and L (No-Bias); incorrect responses were equally penalized with the removal of points. The psychometric function relating the proportion of “long” choices to sample duration was shifted leftward when correct “long” choices produced more points than correct “short”, and rightward when “short” produced more points. Although shifts in the PSE were very small, in the order of tens of milliseconds, this effect was found to be statistically significant. There was no effect of condition on the sensitivity parameter.

Another study that investigated the effects of differential payoffs in humans was conducted by Daniels et al. (2015). Although the manipulation was similar to Akdoğan and Balcı (2016b) in the sense that increases in payoffs meant increases in the number of points for a given correct response, there were also a number of differences, such as no deduction of points for incorrect responses, no test phase, and only two conditions, No-Bias followed by Long-Bias. Additionally, instead of evaluating temporally-controlled behavior after the interval had elapsed, they used a “switch” task, in which participants could respond during the 4-s (S) and 8-s (L) samples, with the first response at the end of the interval reinforced if correct. Thus, on L-trials participants start responding “short” and switch to “long” once enough time has passed, producing a cumulative latency-to-switch function, theoretically analogous to the psychometric function. Interestingly, the shifts were opposite to those found in the literature to date and unexpected to most timing models (e.g., Gibbon, 1977; Machado et al., 2009): participants switched later (instead of earlier) when receiving more points for responding “long”.

Given the small and contradicting effects reported, differential payoff manipulations warrant further investigation in the human timing domain. In the current paper, we describe two experiments varying the reinforcement probabilities for correct “short” and “long” responses in a temporal bisection task with human participants. In Experiment 1, each participant went through three counterbalanced conditions in the same session, Short-Bias, No-Bias, and Long-Bias, each with a training and a test phase. In Experiment 2, participants learned a time-place association in a procedure that allowed the observation of responding during and after the sample intervals. The task was presented as a video game, in which the participant had to move a spaceship to shoot an alien either on the left or on the right, according to the sample duration. The computer tracked the location of the spaceship through time.

To summarize, with these experiments we aim to study the effects of differential payoffs in human timing and analyze how responding in the bisection task relates to behavior as the interval elapses.

Experiment 1

Method

Participants. Sixteen undergraduate Psychology students (between 18 and 23 years old) at the University of Minho in Portugal participated in the experiment for course credits. At the end of the experiment, the participant with the highest score received a gift card from a local bookstore, valued at 10 euros; participants placed second and third received a note pad. Four participants were excluded from the experiment because they did not reach the learning criterion during pre-training (see below); thus only 12 participants were included in data analysis. All participants read and signed an Informed Consent Form. This study was approved by the University of Minho Ethics Subcommittee for Human and Social Sciences (SECSH 054/2017).

Experimental setting. Participants sat in individual sound-proof booths and performed the task in a Desktop Computer, running Microsoft Windows. Stimuli were played through over-ear headphones and responses were recorded from a Cedrus$^{©}$ response pad. The experiment was programmed on SuperLab$^{©}$ software.

Stimuli. Stimuli used in the computer task were 1000 Hz tones generated in Audacity$^{©}$ audio software (version 2.2.2). Tones differed only in duration, with an arithmetic progression (Humans tend to bisect at the arithmetic mean, e.g., Wearden & Ferrara, 1996): 500, 540, 580, 620, and 660. 500 ms was the short duration (S), and 660 ms was the long duration (L) used during training (anchors). The intermediate sample durations, 540, 580, and 620 ms were later added as testing probes.

Durations were chosen to avoid counting and induce perceptual uncertainty. Participants should be able to discriminate between anchor stimuli, but intermediate stimuli should be similar enough to create some doubt when responding. Pilot studies conducted in the laboratory attested that the 40 ms steps used between durations permitted good discrimination between the anchors while creating uncertainty concerning the existence of intermediate durations.

Procedure. Prior to the experiment, participants were instructed (on paper) to listen to the tones and to choose between two keys in the response pad, marked "S" or "L", when question marks appeared on the screen. They were requested to respond quickly and precisely, and to avoid counting or conducting rhythmic activities during the presentation of the sound stimuli. Instructions also contained the following note: "It is possible that at some point during the experiment you might feel that you are pressing one of the keys more often than the other. You shouldn't worry about this; always try to do the best you can." This was an attempt to avoid participants changing their behavior to distribute responses more evenly instead of responding according to their perception of the stimuli presented. All instructions were in Portuguese.

After reading the general instructions, participants entered the cabins. There, they received further computerized instructions, with one short sample followed by "This was a short tone" displayed on the screen; the equivalent was shown for the long sample.

Participants were then exposed to three different experimental conditions of a temporal discrimination task: Short Bias (SB), Long Bias (LB), and No Bias (NB). Order assignment was randomized, with each possible permutation attributed to two participants. Each condition was composed of pre-training, training and test phases. After each condition, participants took a three-minute break outside the soundproof cabins.

Pre-training. This phase presented blocks of ten randomized trials, 5 S and 5 L, until the participant completed one full block with no errors. Participants were informed that points were not available but that they had to succeed to proceed to the next phase, in which they would be able to get points. Correct responses were followed by the word "Correct!" displayed on the screen for 1 s and incorrect responses were followed by a blank screen for 1 s. Intertrial intervals were one second on average, ranging from 0.5 to 1.5 s in steps of 0.25 s.

A maximum of 30 errors was allowed. Participants exceeding this number were considered not to have reached the learning criterion and did not continue to the next phases. We also excluded them from all data analyses. This phase occurred before each experimental condition and ensured that every participant would begin each manipulation with comparable stimulus discrimination.

Payoff Training. Computer instructions informed participants that in this phase they would be able to gain points but that not every correct response would receive feedback. They were also encouraged to win as many points as possible.

This phase introduced the payoff manipulations shown in Table 7. In LB, a “long” response was more likely to be reinforced than a “short” response, given that a response was correct; with *p*, the proportion of reinforceable, or baited, short trials = 0.2 and *q*, the proportion of baited long trials = 0.8. In NB, the proportion of baited trials was equal in short and long trials (both 0.5). In SB, *p* was higher than *q* (0.8 vs. 0.2, respectively). The delta values shown in the table correspond to the payoff differentials, $\Delta = p - q$.

Table 7

Structure of the Blocks of Trials, with Number of Baited Trials, Number of Trials per Type and Corresponding Payoffs, in the Different Phases and Conditions of Experiment 1.

Condition	Phase	Baited trials/Type			Payoff			
		S	L	Probes	*p*	*q*	Δ	Probes
	Pre-training	5/5	5/5	-	1.0	1.0	0.0	-
LB	Training	2/10	8/10	-	.2	.8	-.6	-
	Test			0/6				.0
NB	Training	5/10	5/10	-	.5	.5	.0	-
	Test			0/6				.0
SB	Training	8/10	2/10	-	.8	.2	+.6	-
	Test			0/6				.0

The Payoff Training phase contained 60 trials, which were randomized in blocks of 20 (10 S and 10 L). The base rate, or trial frequency, of short and long samples was maintained equal in all conditions. Sample presentation remained as in pre-training but feedback for correct responses, when displayed, was “+ 1 point” shown on the computer screen. Non-reinforced trials and incorrect responses produced a one-second blank screen, followed by an ITI averaging 1 s in length.

Payoff Test. This phase introduced the three non-reinforced probe trials (540, 580, and 620 ms). Inserting probe trials maintained payoffs for “short” and “long” and only slightly reduced the overall probability of feedback in the test phase compared to the training phase. The test phase had six blocks and a total of 156 trials. Each block consisted of a randomized presentation of 10 S, 10 L, and six intermediate trials (two per intermediate duration).

This phase was planned to introduce the probes smoothly among S and L trials, in order to avoid their detection as obviously neither “short” nor “long”. Thus, the transition from training to testing was not signaled in order to maintain the change inconspicuous.

A counter displayed the cumulative number of points three times during each payoff condition, after every two blocks of training and testing, with a short message encouraging the participant to continue trying to get as many points as possible.

Data analysis. Performance in the test phases was plotted in psychometric functions showing the proportion of “long” responses for each sample duration. We fitted a cumulative normal distribution with four free parameters, α, β, μ, and σ (Equation 1) to each participant’s psychometric function by the method of least-squares. The best-fitting parameters for each participant are included in Appendix G.

$$1 \quad \Psi(t; \mu, \sigma, \alpha, \beta) = \alpha + (1 - \alpha - \beta) F(t; \mu, \sigma)$$

Repeated-measures analyses of variance (ANOVA) with Condition and Duration as factors were conducted for the psychometric functions as well as for the parameters of the fitted functions. The Greenhouse-Geisser correction was used whenever the sphericity assumption was not met. Differences in means were tested with paired-samples t-tests. A significance level of .05 was used in all analyses.

Results and Discussion

In pre-training, the twelve participants who finished the experiment (i.e., all three conditions) went through, on average, 23.8 (*SEM* = 3.4) trials and made 3.8 (±1.0) errors, before moving on to payoff training. Figure 27 shows the average proportion of correct responses for the Short and Long samples obtained in each Payoff Training phase. A repeated-measures ANOVA showed that, as payoff for “long” increased, the proportion of correct responses in L-trials increased, $F(2, 22) = 4.44$, $p = .02$, $\eta_p^2 = .29$. Conversely, the proportion of correct responses in S-trials decreased as payoff for “short” decreased, but the greater variability led to a non-significant effect of condition, $F(2, 22) = 1.10$, $p = .35$. Although p(correct) for S-trials were relatively unaffected in condition SB, overall there is a clear behavioral effect of differential payoffs on the discrimination between the anchor durations.

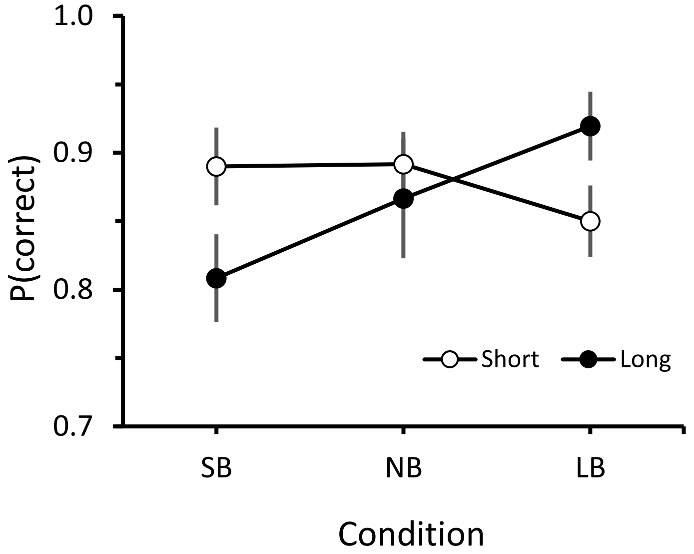

Figure 27. Proportion of correct responses for Short (empty circles) and Long (filled circles) samples (*M* ± *SEM*) for the Payoff Training phase of each condition in Experiment 1.

Figure 28 presents the average proportion of long choices as a function of the sample duration (symbols) from the Payoff Tests, and their corresponding cumulative Gaussian fits (lines). Discrimination of the anchors was not perfect: for S it ranged from .02 to .45 and for L from .45 to 1.00. This confirms results from training, showing that responding at the anchors was affected by experimental conditions. However, the sigmoidal shape of the functions indicates that participants were still overall sensitive to the range of durations. The proportion of long responses increased significantly with sample duration, $F(2.03, 22.89) = 5.37$, $p < .001$, $\eta_p^2 = .91$, and was significantly affected by condition, $F(1.28, 14.02) = 8.50$, $p = .01$, $\eta_p^2 = .44$. The interaction between condition and duration was not significant, $F(8,88) = 1.15$, $p = .34$, since, in general, the three functions plotted in Figure 28 are shifted vertically from each other and do not tend to meet at the anchors.

Figure 29 shows the average parameters (± *SEM*) per condition. Parameters α and β (top left and right, respectively) determine the range of the function: its minimum (α) and maximum ($1-\beta$) and were included due to the differences found among participant and conditions in the discrimination of the anchors. The closer α and β are to 0, the better the discrimination. Although there is an upward trend for α, i.e., discrimination of S decreases as payoff for "long" increases; and downward for β, i.e., discrimination of L increases, the effects of condition did not reach statistical significance, $F(2, 22) = 1.63$, $p = .22$, and $F(2, 22) = 1.07$, $p = .36$, respectively.

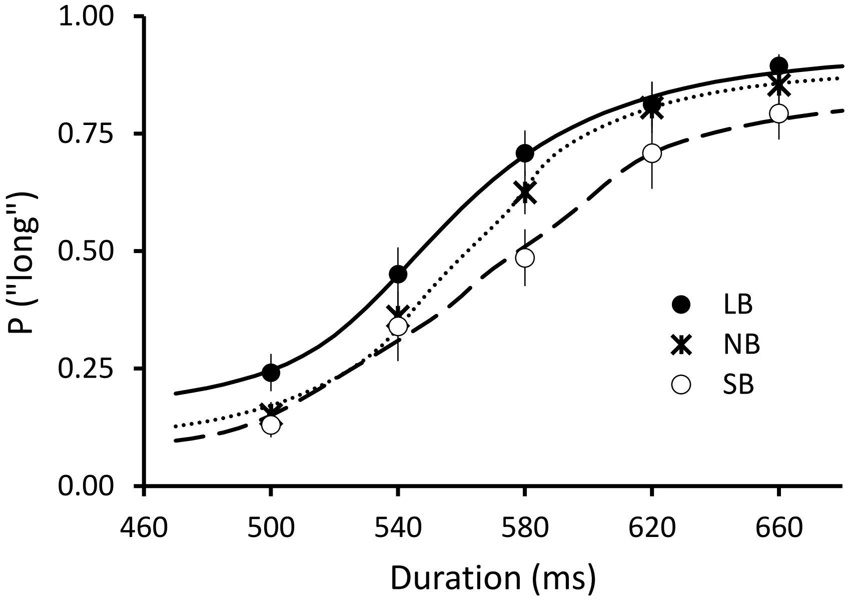

Figure 28. Proportion of "long" responses (*M* ± *SEM*) per sample duration (symbols) and average of individually fitted cumulative Gaussians (lines) for each condition in Experiment 1: LB (filled circles, solid line), NB (asterisks, dotted line), and SB (empty circles, dashed line).

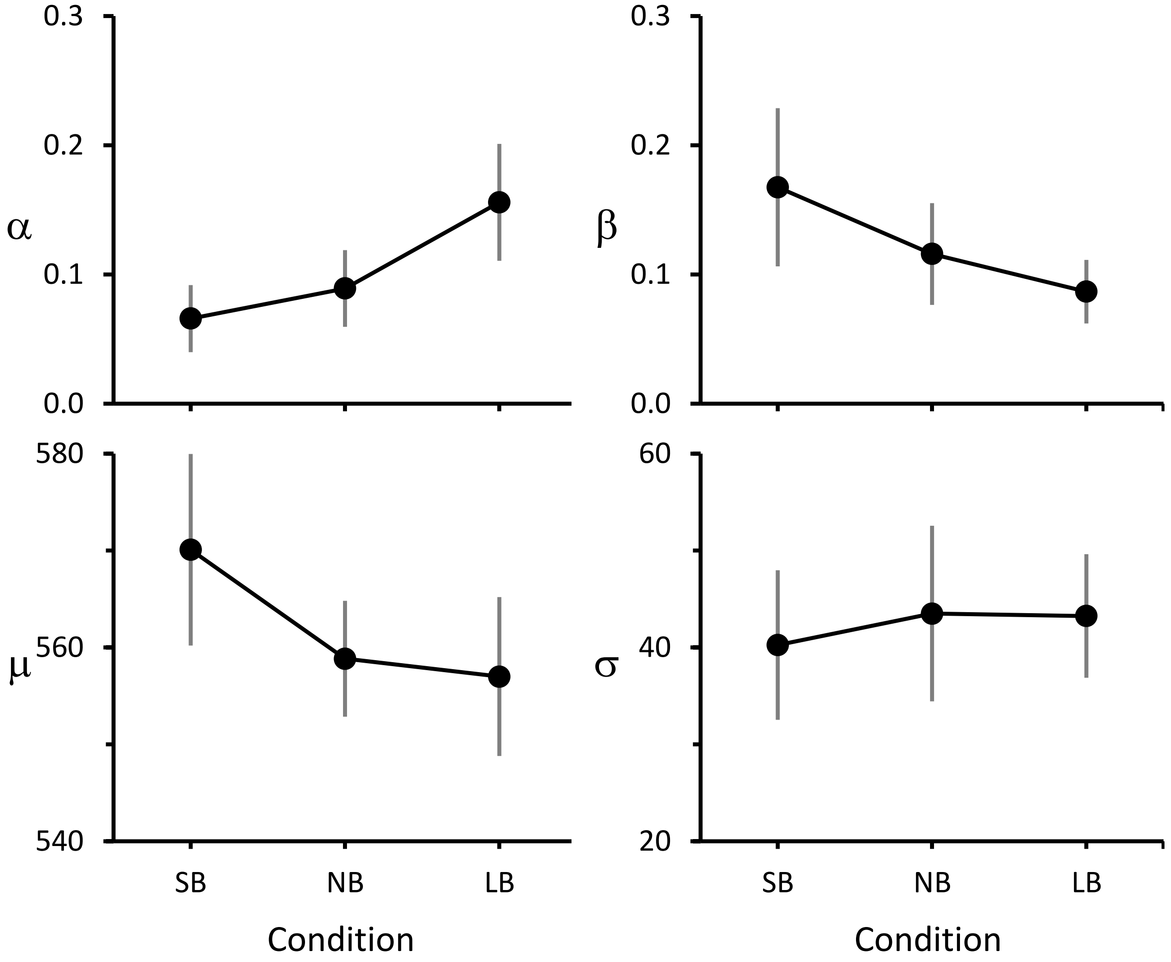

Figure 29. Average of the best-fitting parameters (M ± SEM) per condition in Experiment 1.

The location parameter, μ (bottom left), corresponds to the halfway point between the maximum and minimum, a measure of the PSE. This parameter decreases, on average, with the increase of payoff for "long", in accordance with Figure 28. However, again the differences were not statistically significant, $F(2, 22) = 0.78$, $p = .47$. The scale parameter, σ (bottom right), the inverse of the slope at μ, is an index of sensibility, and there is no indication of a trend in this parameter, $F(2, 22) = 0.04$, $p = .96$. Because of the large variability in participants' performance, it is possible that increasing the number of participants in the experiment could also increase the statistical power to detect possible parameter effects, which a *post-hoc* analysis on G*Power software computed as 0.2 (low).

To confirm the overall effects of payoff on choice (cf. Figure 28), we computed for each condition the proportion of "long" choices during the test phase, averaged across all trials (Figure 30). This analysis confirmed that participant's preference for "long" increased as a function of payoff, irrespective of sample duration, $F(1.26, 13.81) = 8.06$, $p = .01$, $\eta_p^2 = .42$. Together with the parameter analysis, this indicates that payoffs biased responding towards the richer alternative, shifting the function upward (LB) or downward (SB) in comparison to NB.

Thus, although functions were overall different, unlike Akdoğan and Balcı (2016b), there is no clear evidence of changes in the PSE, as measured by μ. Although perceptual bias may be indistinguishable from response bias as measured by differences in the PSE (Raslear, 1985), the increase in "long" responses as payoff for long increased may reflect merely a response bias, with in the subjective perception of the sample durations remaining unchanged.

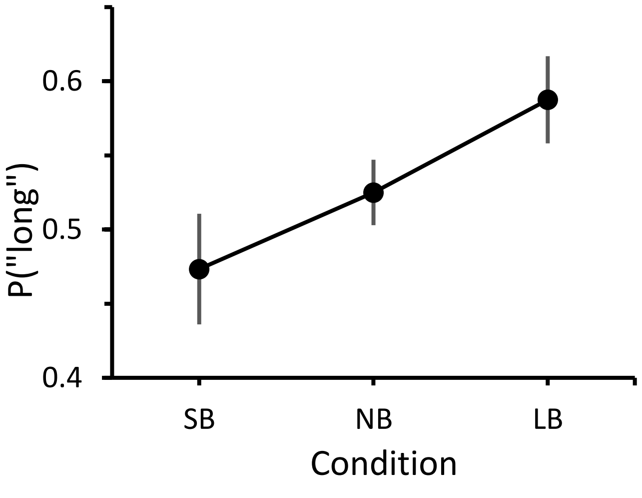

Figure 30. Average proportion of "long" responses (*M* ± *SEM*) per condition and sample duration in the Payoff Test phases of Experiment 1.

Experiment 2

In Experiment 1, participants responded more overall on the key that produced most points, with no independent evidence for a payoff-induced change on time perception. With a modified version of the bisection task, Experiment 2 aimed to observe responding during the sample to see if differential payoffs affect a trial-by-trial decision criterion. Using the two-dimensional space of a computer screen, differences in the moment of moving from the "short" to the "long" side of the screen may, in a sense, "externalize" the timing mechanism that could anticipate or delay the decision to depart towards the "long" side.

Method

Participants. Eight adults (between 25 and 32 years old) volunteered for the experiment during the summer. Two participants were excluded from the experiment and from all data analyses because they did not reach the learning criterion during baseline (see below). All participants read and signed an Informed Consent Form. The study was approved by the University of Minho Ethics Subcommittee for Human and Social Sciences (SECSH 054/2017).

Experimental setting. Participants sat in individual sound-proof booths and performed the task on a Desktop Computer running Microsoft Windows. The experiment was programmed on Visual Basic language, using Visual Studio Express 2010, and ran as an executable file. The task was presented as a computer game with a vintage 1980's aesthetic. Stimuli were played through on-ear headphones and responses were recorded from the computer keyboard.

Stimuli. Stimuli used in the computer task were free sound clips downloaded from soundbible.com in WAV format. Appendix I contains specific information on all sound files used on the task. Sample to-be-timed sound clips were cut using Audacity$^{©}$ software to fit the geometric series: 1 s, 1.3 s, 1.7 s, 2.3 s, 3 s. Thus, 1 s was the short duration (S), and 3 s was the long duration (L). A geometric series was chosen to approximate the stimuli to previous experiments with pigeons (Cambraia et al., 2019; Machado & Keen, 2003). Durations were longer than in Experiment 1 so that participants would have enough time to move the spaceship on the screen during the sample.

Procedure. Each participant went through two experimental sessions of a temporal bisection task. Each session lasted up to 50 minutes each, including signing the Informed Consent and debriefing. Instructions on how to play were presented on the screen at the beginning of every session, but the experimenter responded to any questions until the participant was ready to start. Questions that required more information than available in the instructions, such as “Which alien do I have to shoot?”, were responded with the experimenter paraphrasing relevant parts of the instructions and saying, “Don’t worry, you will learn what to do as you play the game”.

The general trial structure went as follows: Two aliens appeared on each side of the game panel (

Figure *31*A), and a spaceship appeared on the center. Simultaneously, the alien sound clip would play for a given duration. From trial onset, participants could move the spaceship to the right or left by pressing the corresponding arrow keys on the keyboard. At the end of the sample, the spaceship could fire shots by pressing key “A”. To gain points, the participant had to place the spaceship under the correct alien and shoot. Half of the particiants had to choose the left alien following the short sound duration, i.e., S–left, L–right, and the other half had the reverse mapping. Feedback for correct baited trials was the aliens exploding and an explosion sound, as well as gaining 10 points, which were added to the score (

Figure *31*B). Feedback for incorrect trials or for correct non-baited trials was the same: zero points were added to the score (

Figure *31*C) and a whooshing sound played. A dark screen intertrial interval was then presented for 0.5, 1, or 1.5 s, randomly selected.

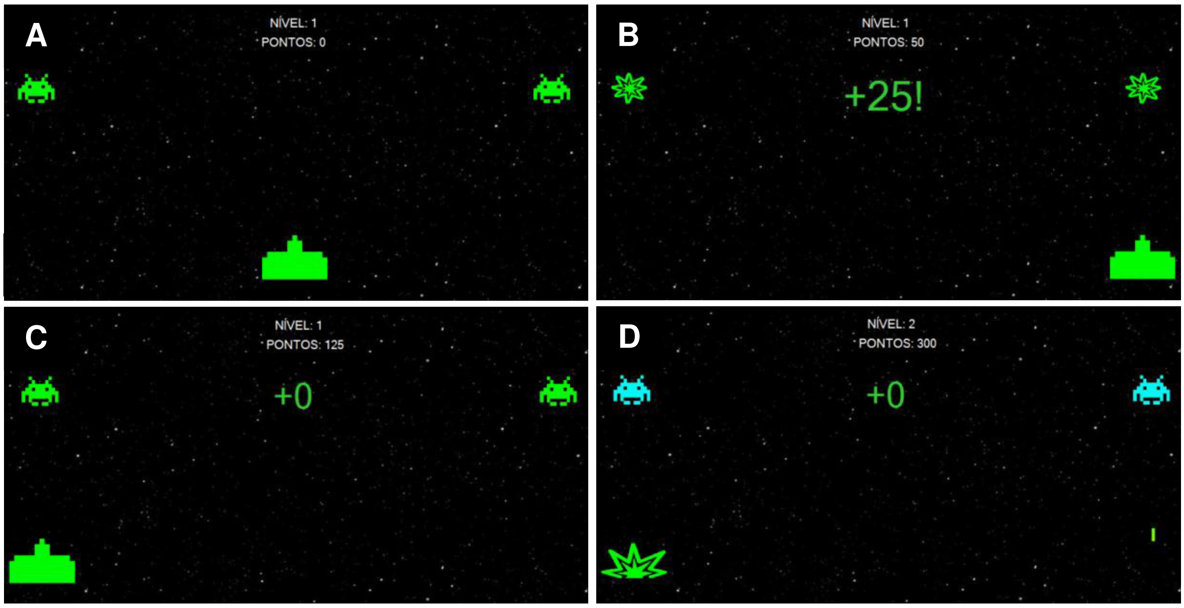

Figure 31. Temporal bisection task game panels from Experiment 2. A) Trial onset; B) Feedback for correct response; C) Feedback for incorrect and non-baited trials; D) Feedback for missed trials.

On each session, participants went through 10 levels. Levels did not always map directly to experimental phases; the test phases in each condition, which included more trials than training, were split into three levels (every four blocks). Introducing level breaks had the goal of motivating the participants to continue in the task and sometimes provided further instructions. The participant had to select “Next” to move on to the next level of the game.

Table 8 shows the experimental conditions and phases for each session. Conditions are labeled according to their payoffs on short and long trials (p–q): CRF (1.0–1.0), NB (0.5–0.5), SB (0.75–0.25), and LB (0.25–0.75). Each condition contained a training and a test phase. Conditions and phases are presented in order of exposure, except LB and SB, which were counterbalanced.

Table 8

Structure of the Blocks of Trials, with Number of Baited Trials, Number of Trials per Type and Corresponding Payoffs, in the Phases and Conditions of Sessions 1 and 2 of Experiment 2.

Condition	Phase	Baited trials/Type			Payoff			
		S	L	Probes	*p*	*q*	Δ	Probes
				Session 1				
CRF	Pre-training Training	6/6	6/6	-	1.00	1.00	.00	-
	Partial reinforcement	4/6	4/6	-	.67	.67	.00	-
	Test	3/3	3/3	0/3	1.00	1.00	.00	.00
NB	Training	2/4	2/4	-	.50	.50	-	-
	Test			0/3			.00	.00
				Session 2				
NB	Training	2/4	2/4	-	.50	.50	.00	-
LB	Training	1/4	3/4	-	.25	.75	-.50	-
	Test			0/3				.00
SB	Training	3/4	1/4	-	.75	.25	+.50	-
	Test			0/3				.00

Session 1 – Overall payoffs. In this session, participants learned the temporal bisection task as they played the game and reinforcement was progressively reduced to 50% per sample so that, in Session 2, introducing the payoff differential was not affected by the overall loss of points. Session 1 had six phases: Pre-training, Training, Partial Reinforcement, Test, NB Training and Test.

Pre-training. This phase presented one block of twelve randomized trials, 6 S and 6 L. If participants made more than one error per sample, the block repeated (repetition criterion), for a maximum of 8 repetitions (exclusion criterion). Else, they moved to the next phase. These criteria remained for every training phase in the experiment and were removed on every test phase.

Training. This phase was the same as the previous one, except that a Limited Hold (LH) of 1 s per sample was added. In other words, participants had to kill one alien up to 1 s after the sample ended, i.e., 2 s after S-trial onset and 4 s after L-trial onset. If they did not, the aliens would shoot down, the spaceship would explode, and zero points were added to the score (

Figure *31*D). These trials were considered errors for the repetition criterion. This contingency was added to motivate participants to move the spaceship during the sample. The LH was maintained throughout all training phases of the experiment.

Partial reinforcement. This transition phase was added to prepare participants for the reduction in overall reinforcement in the test phase that followed. It was exactly as the previous phase except only 67% of the trials were baited.

Test. In this phase, each block had 3 S, 3 L trials, and 3 probes, one of each intermediate duration (1.3, 1.7, 2.3 s). Probes were never reinforced. During this and all subsequent test phases, LH was set to 10 s so that participants would have time to move the spaceship around without being killed while at the middle locations between short and long. All responses to the anchors were reinforced, provided they were correct. Thus, the overall probability of reinforcement was 67%.

NB Training. Each block had 4 S and 4 L, half of which were baited. Each participant went through at least two blocks. The repetition and exclusion criteria were only applied from the second block.

NB Test. Each block had 4 S and 4 L, half of which were baited, plus 3 probes, none of which were baited. This phase occurred for a total of 12 blocks, or 132 trials.

Session 2 – Differential payoffs. Session 2 had six phases: NB Training, SB Training, SB Test, NB Training, LB Training, LB Test. Conditions LB and SB were counterbalanced so that half of the participants went through LB first and the other half went through SB first.

SB Training and Test. In these phases, payoffs were greater for S (0.75) than L (0.25; see Table 8). These were otherwise the same as NB Training and Test (Session 1).

LB Training and LB Test. In these phases, payoffs were greater for L (0.75) than S (0.25; see Table 8). These were otherwise the same as NB Training and Test (Session 1).

NB Training. This phase was the same as in Session 1 and occurred twice during the session, once before each differential payoff condition. Its purpose was to make sure that the participant was still able to perform the task at the start of the session and was also a transition phase between conditions, as an attempt to minimize possible carry-over effects.

Results and Discussion

In pre-training, the six participants who finished the experiment went through 26 trials on average (± *SEM* = 4.82), in a minimum of one block and a maximum of three, and made an average of 7.50 (±2.54) errors. When the limited hold was first added (CRF training), each participant went through two blocks, except P6, who did three (26 ±2 trials). On average, they missed 28% (±3) of the trials, i.e., did not respond within the limited hold.

P("long"). The proportion of "long" choices for the training phase of each condition is shown in Figure 32, including for CRF. Although on average the overall proportion of "long" responses for condition NB (filled circle) increased compared to CRF (empty circle) this difference was non-significant, $t(5) = 0.591$, $p = .58$. Also plotted are data from conditions SB and LB (both from session 2). As the payoff for "long" increased and the payoff for "short" decreased, the proportion of "long" responses increased on average, but a repeated-measures ANOVA revealed that the effect of condition was not statistically significant, $F(2, 10) = 1.26$, $p = .33$.

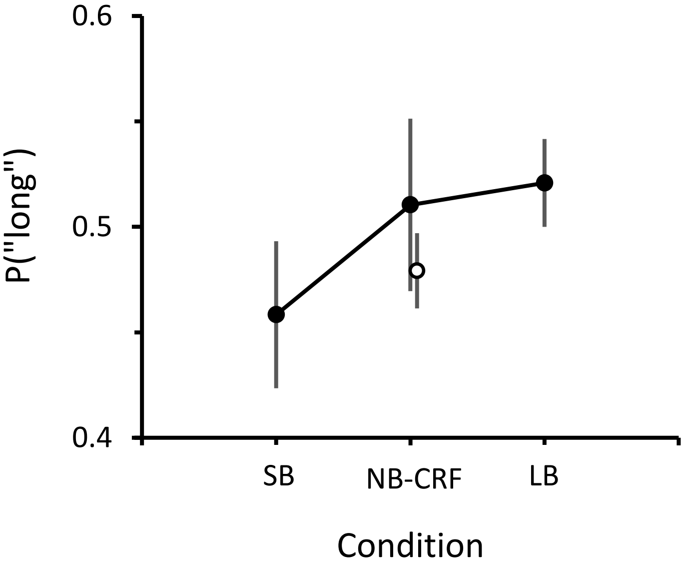

Figure 32. Average proportion of "long" responses (*M* ± *SEM*) for the last two blocks of the Training phases in each condition. Empty circle indicates average for condition CRF.

The psychometric functions (and their corresponding fits from Equation 1), from the test phases of each session and condition are shown in Figure 33. CRF and NB (top panel) produced similar sigmoidal curves, with the one from NB flatter than the one from CRF. A repeated-measures ANOVA with sample duration and payoff condition as factors, revealed a significant effect of sample duration, $F(1.38, 17.93) = 7.91$, $p = .01$, $\eta_p^2 = .38$, but returned no significant effect of condition, $F(1, 13) = 0.73$, $p = .41$, nor of the interaction between factors, $F(2.64, 34.28) = 2.35$, $p = .10$. The bottom panel of Figure 33 shows the corresponding data for conditions SB and LB. An ANOVA with the same factors revealed significant main effects of both sample duration, $F(2.19, 10.94) = 51.11$, $p < .001$, $\eta_p^2 = 0.91$, and condition, $F(1, 5) = 11.78$, $p = .02$, $\eta_p^2 = .70$, but no significant interaction, $F(4, 20) = 1.70$, $p = .19$.

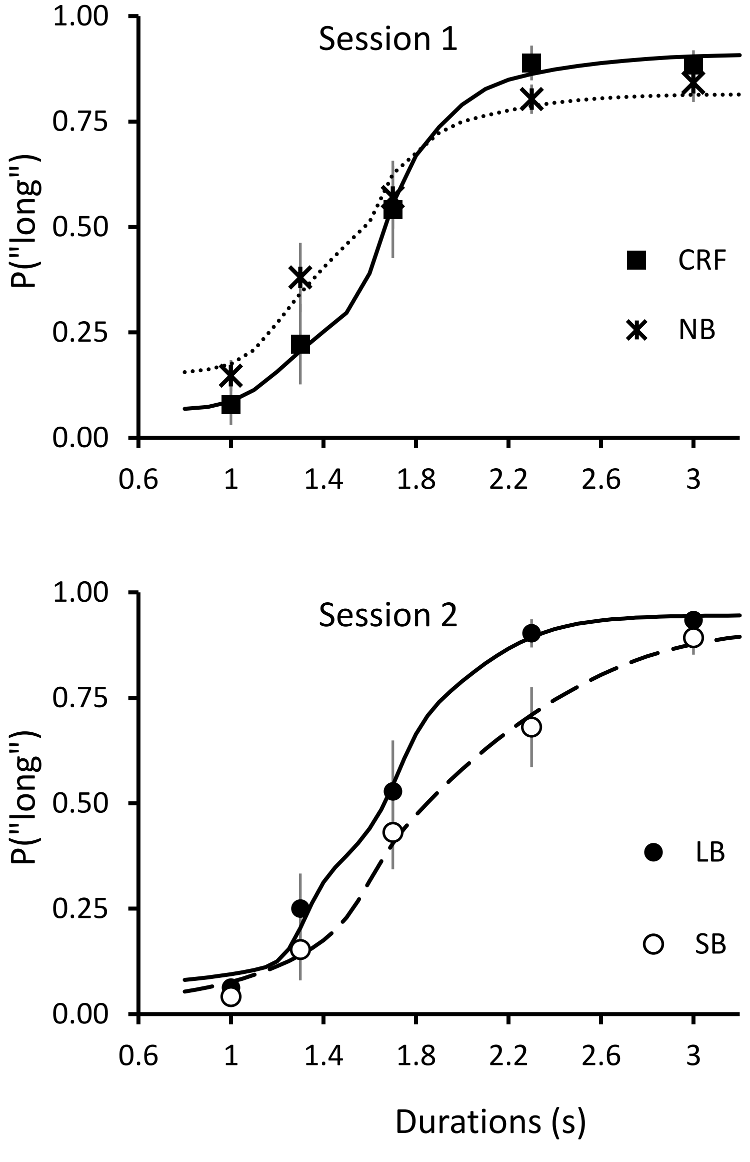

Figure 33. Proportion of "long" responses (*M* ± *SEM*) per sample duration (symbols) and average of individually fitted cumulative Gaussians (lines) for each condition in Experiment 2. Top: Session 1 – CRF (filled squares, solid line) and NB (asterisks, dotted line). Bottom: Session 2 – LB (filled circles, solid line) and SB (empty circles, dashed line).

In sum, while reducing overall payoff seems to flatten the psychometric function, which could indicate a loss in sensitivity, testing with differential payoffs produced shifts consistent with a bias effect, with participants responding more "long" when it provided more reinforcement than "short". The four best-fitting parameters, averaged per condition, are shown in Figure 34 for a finer analysis (refer to Appendix H, Table H1, for individual data).

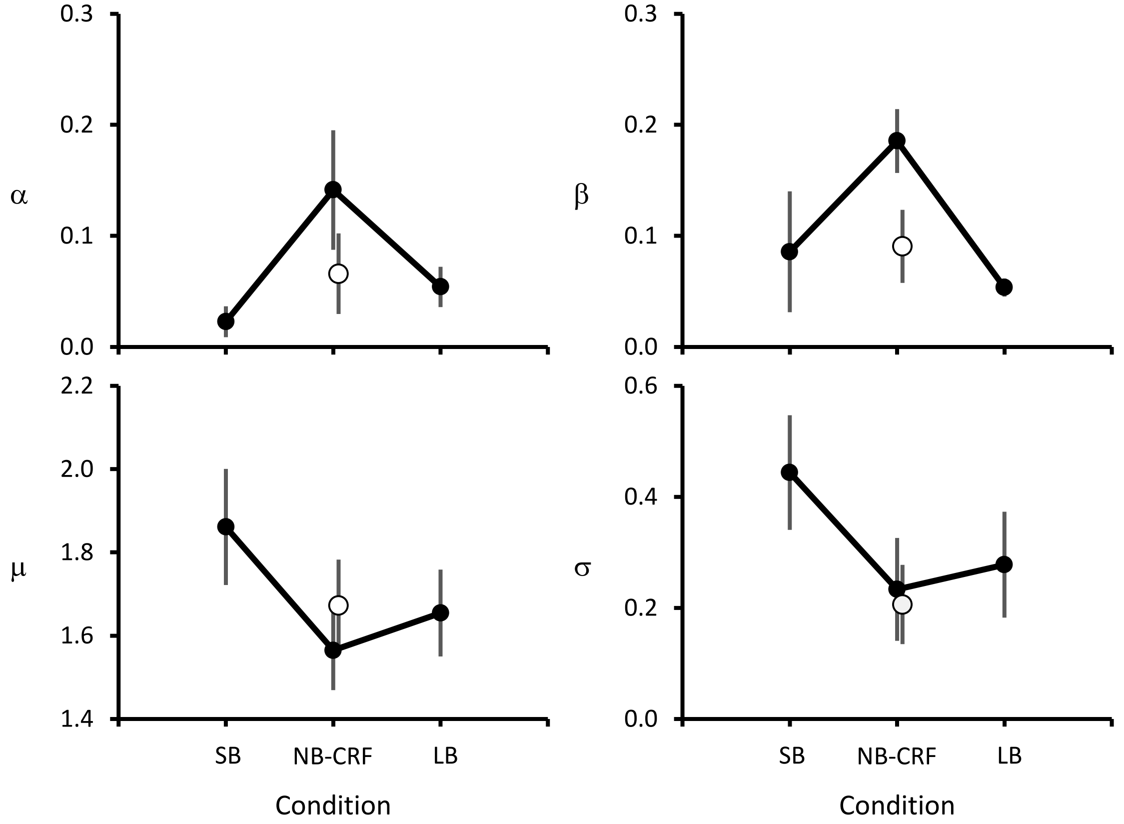

Figure 34. Average best-fitting parameters (*M* ± *SEM*) per condition in Experiment 2. Empty Circle represents CRF.

Condition CRF, which produced a psychometric function similar to NB (Figure 33), is plotted in Figure 34 as empty circles, for further comparisons of the effect of the overall reduction in payoff from CRF to NB. A paired-samples t-test confirmed a loss of discrimination for the L sample (3 s, parameter β, top right) in condition NB compared to CRF, $t(5) = 2.57$, $p < .001$, $d = -4.15$, 95% CI [-6.75, -1.54]. Tests on parameter α (top left) did not reach statistical significance, $t(5) = 1.48$, $p = .20$; thus, there is no real loss of discrimination of S (1 s) in condition NB. There was no significant change on sensitivity (parameter σ), $t(5) = 0.31$, $p = .77$, or bias (parameter μ), $t(5) = 1.39$, $p = .23$.

Conditions with intermittent payoffs are comparable to those of Experiment 1 and plotted with filled circles, in order of increasing payoffs for “long”: SB, NB, and LB. The graphs presenting parameters α and β show that discrimination is good in conditions with differential payoffs, with little variability between subjects. On the other hand, NB appears to produce a loss of discrimination, although only parameter β presents a significant effect of condition, $F(2, 10) = 4.15$, $p = .05$, $\eta_p^2 = .45$. Location (μ) and scale (σ) parameters show a decreasing trend, as payoffs for “long” choices increase, with average SB slightly above LB. However, only μ was significantly affected by experimental condition, $F(2, 10) = 4.89$, $p = .03$, $\eta_p^2 = .50$.

To conclude, reducing overall reinforcement from condition CRF to NB affected discrimination at the anchors, especially for the L-sample. However, because in Session 2 discrimination at the anchors was close to perfect, it is likely that the decrease in “long” for L-trials in Session 1 was a transient effect of the decrease in overall payoff. Although previous studies have observed transient effects of overall reduction of reinforcement on sensitivity to time (e.g., Bizo & White, 1994b), we did not observe changes in the scale parameter of the functions. Increasing payoffs for “long” in condition LB increased the proportion of “long” choices compared to SB, shifting the function leftward, which was confirmed by an effect on parameter μ. This is consistent with a biasing account and replicates findings from the literature (e.g., Akdoğan & Balcı, 2016b).

Motion patterns. To analyze the motion patterns during the sample, we selected six equidistant points in the response panel. Every time the spaceship crossed a point, its location and time were recorded with a resolution of 10 ms. Let us assume that, for all participants, the *short* and *long* sides correspond to locations 1 and 6, respectively. Let $\lambda(t)$ denote the spaceship’s location at time t, with $\lambda(t) = 1, 2, \ldots, 6$, and $0 \leq t \leq$ sample duration, with t measured in 100 ms slices. Since the spaceship location at trial onset was always at the center, $\lambda(0) = 3.5$ on every trial.

For each trial, we obtained a set of relevant motion parameters, namely, Arrival Time at the *short* side (AT), Residence Time at the *short* side (RT), and Departure Time to the *long* side (DT). We defined AT_S as the time since sample onset at which $\lambda(t)$ reached its minimum value (i.e., the time it was closest to the *short* side). For example, if the spaceship moved from the center to the *short* side such that λ(t) = 1 for the first time at t = 0.8 s, then AT_S = 0.8 s. If the participant later moved to λ(t) = 6, we defined the DT as the time the spaceship crossed λ(t) = 1 again. Finally, we defined the RT as the difference between DT and ATs (RT = DT — AT). Note that not all trials will necessarily compute all parameters.

Figure 35 shows the motion patterns during L samples for the first block of pre-training (left), the first block of training (center), and the last block of training (right), for two representative participants (rows). Solid lines are the median locations while dotted lines are the quartiles, indicating variability. From left to right, the panels show how participants learn to move during the sample. Initially, participants tend to stay around the center for at least 2 s, and after moving they don't necessarily go to the correct side, *long*. Then, a clearer pattern begins to emerge, where they tend to remain at the center until the short duration has elapsed, then move to the *long* side, arriving before the long sample has elapsed.

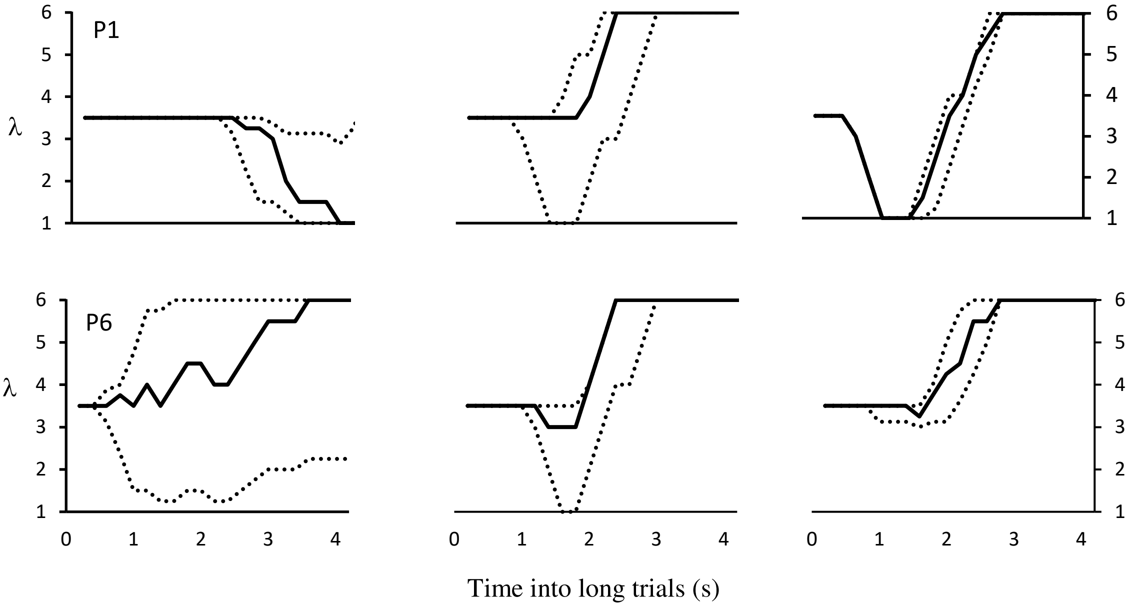

Figure 35. Motion patterns during long sample trials for pre-training and CRF training for 2 participants (P2 on the top, P6 on the bottom) in Experiment 2. The solid lines represent the medians and the dotted lines the quartiles of the location (λ; 1 is "short" side and 6 "long" side) in function of time. Left – first block of pre-training; center – first block of training; right – last block of training.

Finally, most participants learn to move to the *short* side first, wait a few seconds, and then move to the *long* side. However, unlike the other participants, P6 learned to remain near the center, moving only past λ(t) = 3, before departing to *long* (cf. bottom row). This was possible because, with a 1-s limited hold, participants still had enough time to arrive at the *short* side without being killed after the sample had elapsed. In the last block of training, average AT = 1.48 s (± 0.3), RT = 0.52 s (± 0.05), and DT = 1.72 s (± 0.03).

Median motion patterns for each participant in conditions LB (solid curves) and SB (dashed curves) are depicted in Figure 36. Three participants (P2, P3, and P5) maintained the *short-long* pattern on most trials for both conditions, despite the removal of the limited hold during testing. While P3 and P5 would depart to *long* about 200 ms earlier when that side had most reinforcers (LB), compared to when it had fewer (SB); P2 showed the reverse, by departing earlier in SB. P6 maintained the center-*long* pattern and departed about 400 ms earlier in LB compared to SB. P4 probably learned that the limited hold had been removed and stopped moving to *short* at trial onset. This participant showed a similar pattern to P2, by departing earlier in SB. P1 produced the *short-long* pattern during LB and still departed earlier in LB than SB.

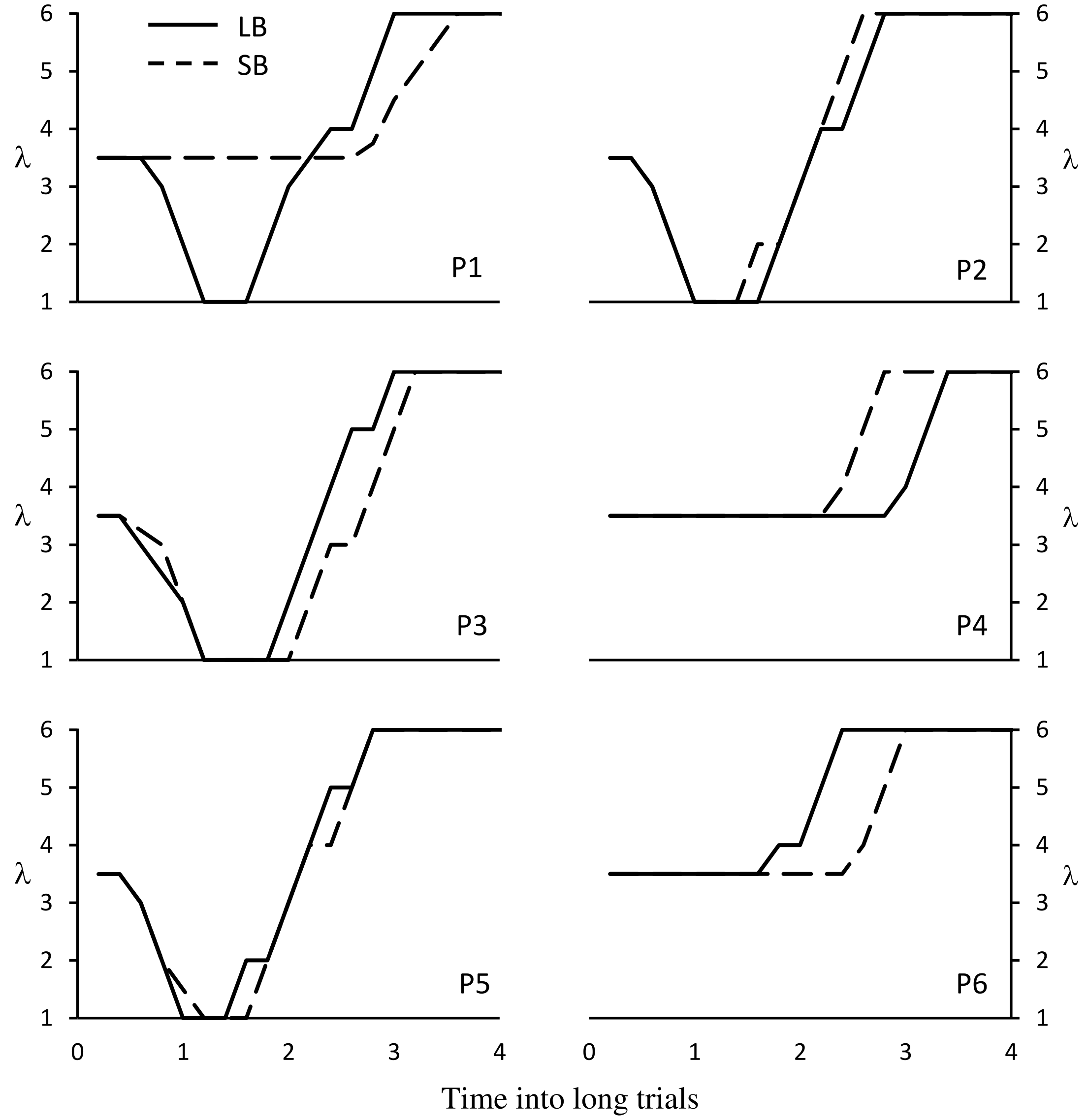

Figure 36 . Individual motion patterns (median only) during long sample trials for conditions SB (dashed line) and LB (solid line) tests in Experiment 2.

In sum, despite showing two different patterns, all participants started motion of the spaceship before the L sample had elapsed. On average, AT = 1.40 s (± 0.22) and RT = 0.43 s (± 0.10) for condition LB and AT = 1.64 s (± 0.24) and RT = 0.32 s (± 0.12) for condition SB. While four departed earlier when "long" produced higher payoffs, two departed later, with average DT = 1.81 s (± 0.16) in LB and 1.91 s (± 0.15) in SB. Differences between conditions in the motion parameters did not reach statistical significance.

Departure times and P("long"). The moment the spaceship departs toward the *long* side may be considered a measure of indifference between short and long durations in the bisection task, analogous to the PSE; just before departing, the participant behaves as if the sample was short and at the DT the participant behaves as if the sample was long. Figure 37 compares the average cumulative distribution function of DTs (lines) with the average psychometric function (symbols). Conditions CRF (top left) and NB (top right) show a good approximation between these measures, except for the long sample where the cumulative distributions overestimate choice. Individual data are presented in Table H2, Appendix H The bottom graph compares data from the differential payoff conditions. On average, participants departed earlier towards the *long* side in LB. Interestingly, the 2.3-s sample, which corresponds to the greatest difference in p("long") between conditions, is not associated with a notable difference in the distribution of departure times. This indicates that, although on 80% of the trials the spaceship had departed towards *long* at 2.3 s or earlier, on about 10% of those trials the participants reversed their motion and chose "short".

In summary, Experiment 2 replicates with human participants results from Machado and Keen (2003). As their pigeons, most of our participants learned to move to the *short* side at sample onset, wait for the S interval, then depart to *long.* Also, DT became a good estimator of the PSE. However, because participants would not always stereotypically move all the way to the *short* side, we defined DT as the point of inflection before moving to *long*, independently of $\lambda(t)$.

These data show similarities to a previous experiment with pigeons (Cambraia et al., 2019). Pigeons departed earlier towards the *long* side when it offered more payoffs, compared to when it offered fewer. Additionally, the distribution of DT and the proportion of "long" choices mismatched during biasing conditions (higher payoff for short or long), although our human participants mismatched mostly in the Short-bias condition.

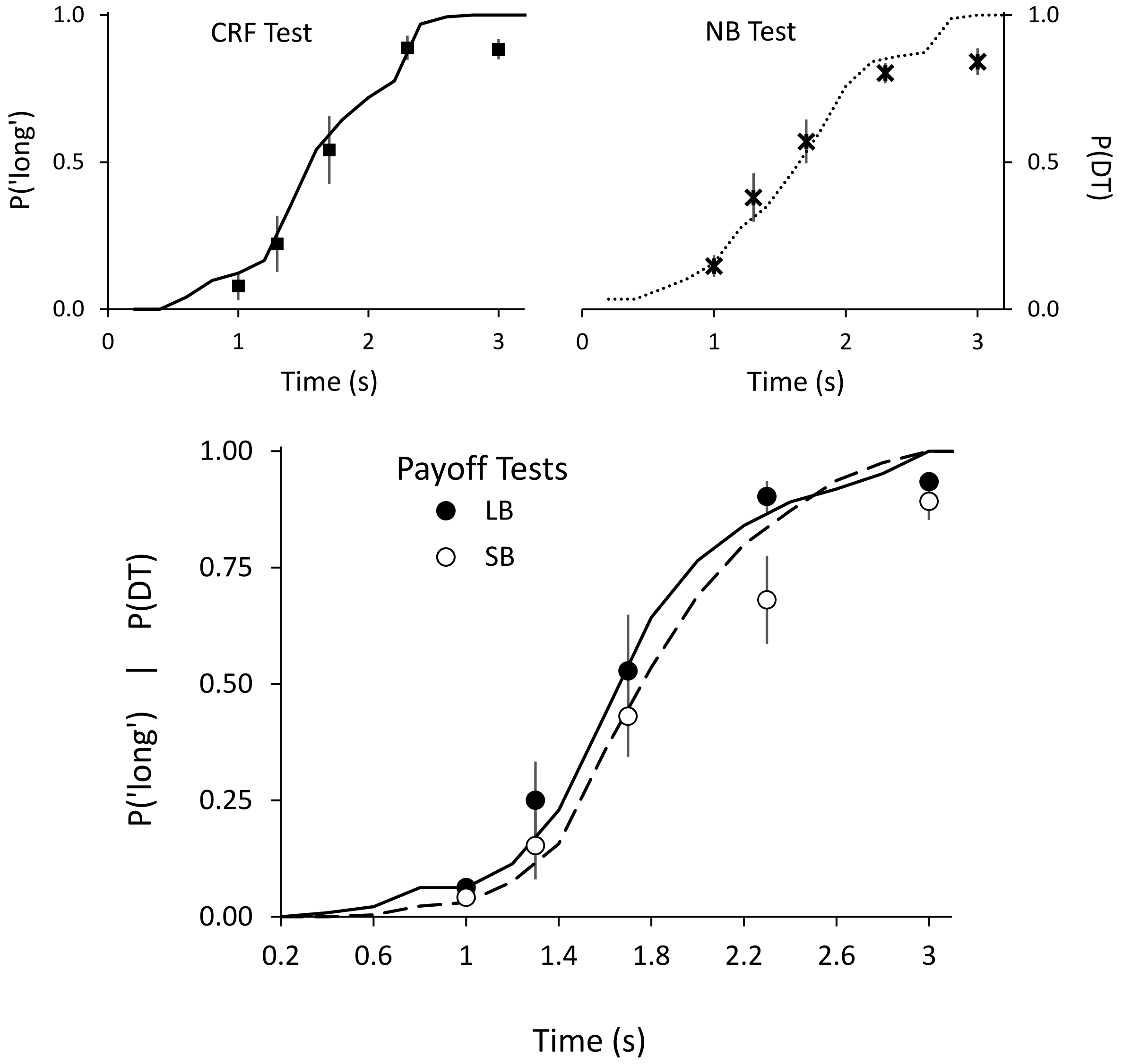

Figure 37. Averaged empirical cumulative distribution function of departure times (lines) plotted against the proportion of "long" (symbols). Top-left: CRF. Top-right: NB. Bottom: LB (solid line, filled circles) and SB (dashed line, empty circles).

General Discussion

The present study investigated the effects of differential probabilities of reinforcement for "short" and "long" responses in a bisection task with human participants. In Experiment 1, participants went through the standard bisection task, learning a symbolic duration—button mapping, then trained and were tested on two conditions with differential payoffs and one with equal payoffs. In Experiment 2, we adapted the task to a time—place mapping (e.g., S—left, L—right) in the context of a videogame with a spaceship that the participants displaced horizontally, enabling us to record location throughout the timed intervals.

We computed psychometric functions based on “long” choice proportion in order to measure the effects of varying the payoff differential. Best-fitting location (μ) and scale (σ) parameters were estimated as measures of response bias and temporal sensitivity, respectively. Asymptotes at the short (α) and long (β) intervals measured discrimination of the anchors. In Experiment 2, we also computed the empirical cumulative distribution functions of departure times to relate the motion patterns during the sample to choice behavior after the sample.

Our data confirmed that differences in relative reinforcement between short and long samples in a bisection task affect the temporally controlled behavior of humans. In Experiment 1, participants increased their overall proportion of “long” choices, displacing the psychometric function vertically. However, there were no significant bias effects as measured by μ. In Experiment 2, p(“long”) increased only for intermediate durations, shifting functions horizontally and thus affecting μ. None of the experiments found any trend or differences in sensitivity.

Two differences in procedure may explain the difference in the results from Experiments 1 and 2. Firstly, the discrimination in Experiment 1 was much harder than in Experiment 2. While durations in Experiment 1 were very short with a ratio of only about 0.75:1, Experiment 2 not only had longer durations, but the ratio was 1:3. In Experiment 1, although discrimination was not lost, some subjects had worse performance at one of the anchors for one or more conditions.

Secondly, the time—place mapping of Experiment 2 may also have contributed to maintaining the anchor parameters, with discrimination close to perfect and smaller variability between participants. Because participants tended to move during the sample, at the time the anchors elapsed the spaceship was very likely to be under the corresponding alien, cueing the participants to choose (shoot at) that location. Thus, in a sense, the location of the spaceship acts as an external clock. It is possible that changes in μ can only be found when the anchors are relatively unaffected by conditions, as in Experiment 2 and previous experiments (e.g., Akdoğan & Balcı, 2016b).

In Experiment 2, participants learned to move during the sample, similarly to pigeons (Machado & Keen, 2003). However, while pigeons tend to be motivated to produce the effort of moving to the *short* side as fast as possible to obtain food, due to deprivation throughout the experiment, humans are offered only a generalized reinforcer, points, which have no immediate value other than information. Because motion during the sample is maintained through a negative reinforcement contingency, i.e., to avoid getting shot at by the aliens, when these contingencies are removed, or "loosened" (increase in the limited hold criterion), some participants may come to realize they are not getting shot at and thus reduce the effort of moving all the way to the *short* location.

When exposed to differential payoffs, most participants departed earlier to the *long* side in LB compared to SB. However, for two participants the pattern was reversed. Although Daniels, Fox, et al. (2015) found a similar reversal with their participants, this phenomenon is not easy to explain, especially in terms of timing mechanisms. Because the reversal only occurred to participants exposed to LB before SB, it is possible that learning interfered. While learning this task, the tendency is for patterns to become more stereotypical and for departure time to decrease. The idea would be that, as the perception of the short duration becomes more precise, the more likely the participant is certain that it has elapsed, and thus will depart to *long* quite soon after that interval. While pigeons are exposed to many sessions within the same condition, before changing, all human participants were exposed to only two sessions of learning, during which they experienced multiple changes in the contingencies of reinforcement, having to adapt in only a few trials.

In general, our findings are in accordance with previous studies in the literature with human and non-human animals (e.g., Akdoğan & Balcı, 2016b; Machado & Guilhardi, 2000; Stubbs, 1976) in showing that differential payoffs can affect temporal discrimination. This study not only contributes to generalize the results to different contexts of supra-second intervals (Experiment 1) and time-place associations (Experiment 2), but also to bring to light issues of between-subject variability and differences between species.

The distribution of reinforcers in a session did not produce significant changes in sensitivity, but biased choice and departure times, in addition to reducing overall temporal control. More experiments should be conducted in order to refine our knowledge of the effect detected in this study, to which theory will need to be confronted. Yet, the confirmation of payoff-related biasing effect in the bisection task favors a behavioral account of timing over a cognitive one. In the cognitive perspective (i.e., SET), reinforced intervals in the bisection task are saved in two memory distributions, one for "short", one for "long", from each of which subjects recall a sample at the onset of a trial. Responding "short" or "long" is selected regarding the resemblance of the perceived interval at the end of the sample trial as compared to the sample drawn from memory. In this view, the distribution of the samples in memory does not depend on the number of samples. That is, the average sample selected from each distribution is independent of differential reinforcement for “short” and “long” intervals. To account for a biasing effect, SET needs to add to its original structure a bias parameter sensitive to the probability of reinforcement (e.g., Jozefowiez et al., 2014).

On the other hand, from the viewpoint of behavioral models of timing such as LeT, reinforcement of “short” and “long” trials create vectors of associative links relating both “short” and “long” responses to the elements composing a chain of time-dependent behavioral events. The response emitted at the end of the sample depends on the relative strength of the associations between the behavioral state active at that time and each of the responses. Thus, more payoff following one of the two intervals will strengthen the vector of associative links of the corresponding response, increasing the number of behavioral states susceptible to sustain that response over its competitor, thus biasing responding. This account of the effect of differential payoffs is free of modifications to the original principles in a behavioral framework of timing.

CHAPTER V

DIFFERENTIAL BASE-RATE EFFECTS ON HUMANS

I would like to thank Mehdi Bugallo for help planning and collecting data for Experiment 1.

Abstract

We investigated how differential base-rates affect temporal discrimination. In a temporal bisection task, humans learned to make one response after a short sample and another after a long sample. When presented with a range of intermediate samples they produced a Gaussian-like psychometric function characterized by a location (bias), a scale (sensitivity) parameter, and two asymptote (discrimination) parameters. In Experiment 1, the location parameter changed, with half of the participants biasing their choice in the direction of the response associated to the most frequent sample, and half showing the opposite pattern. In Experiment 2, when we used a simple video game to track motion during the sample, the patterns became highly stereotypical – on the long sample trials, participants approached the "short" response location at sample onset, stayed there for a while, and then departed to the "long" location. The distributions of departure times were biased, with early departures toward the "long" option, but the psychometric functions were not, thus exposing a dissociation. These results suggest methodological recommendations for the study of interval timing in human participants and contribute to our understanding of the basic mechanisms involved in interval timing and learning.

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Researchers have been demonstrating the accuracy with which humans and non-human animals are able to estimate short intervals of time (milliseconds to minutes), since as early as the 19th century (James, 1890). A rich set of procedures to study time perception has enabled the collection of considerable data, which has been translated into a set of properties that characterize subjective time (for reviews, see Church, 2002b; Lejeune et al., 2006; Richelle & Lejeune, 1980).

The existence of such properties may lead to the impression that time perception is rigid and absolute and although researchers have noted that this is not necessarily the case, only towards the late 20th century has interest renewed in studying how subjective time is flexible and relative by using a variety of tasks (e.g., Maia & Machado, 2009; Morgan et al., 1993; Raslear, 1985). One such task, the temporal bisection, is commonly used to study the discrimination of two or more intervals of time. This task presents a sample stimulus for a specific duration after which two manipulanda, e.g., response keys, are presented. Subjects are then required to choose the corresponding key: short-interval samples are correlated to one key (e.g. "S" on keyboard or "red" pecking key) and long-interval samples to another (e.g., "L" on keyboard or "green" pecking key). Once subjects discriminate the two intervals, they are presented with intermediate samples and their preference for one of the keys is measured. This closely resembles psychophysical procedures developed to quantify perceptual judgments (e.g., Gescheider, 1985).

The typical result is an sigmoidal psychometric function – preference for the "long" key increases from about 0 to about 1 with stimulus duration (Church & Deluty, 1977). The estimated time at which responding is equally likely to occur on the short and long keys, is often referred to as the point of subjective equality, or PSE. Horizontal shifts of the functions (mantaining all parameters constant except for the PSE) indicate biased responding towards one of the keys. An additional advantage of using the bisection task is that it allows measurements of the slope of the psychometric function – a flattened slope at the PSE indicates loss of sensitivity to the sample durations (Blough, 1996).

A still poorly understood question is whether and how non-temporal factors may affect timing. While base-rate manipulations are commonplace in a Signal Detection Theory (Green & Swets, 1966) approach to perceptual judgements (e.g., Maddox & Bohil, 1995, 1998a, 1998b), few studies have examined whether human timing is affected by the relative frequency of presentation of the short and long samples in temporal discrimination. For instance, Jozefowiez et al. (2014) assigned participants to either a No-Bias group or to groups that differed in the relative number of presentations of short (1 s) and long (1.5 s) samples in a bisection task: Long-Bias (twice as many L than S trials) and Short-Bias (twice as many S than L trials). During testing with intermediate durations, Long-Bias participants responded more "long" overall, shifting the psychometric function to the left of the No-Bias function, resulting in a lower PSE. Short-Bias produced a rightward shift, with fewer "long" choices (and thus a higher PSE). No changes in sensitivity were reported.

Anecdotal experience of the passage of time as "slowing down" or "speeding up", suggests that perceptual shifts should occur at an individual level. Çoşkun et al. (2015), confirmed this claim using a within-subject design and a broad range of differential base-rate values. They found that the PSEs monotonically decreased with an increase in the proportion of L trials. However, participants were informed of which experimental condition they would be exposed to on each session.

In the preparation used here, participants were not informed when they entered the test phase of each experimental condition, and reinforcement given a correct choice was intermittent, thus increasing uncertainty of whether non-reinforced responses were correct but non-reinforced, incorrect, or intermediate (neither correct nor incorrect). Additionally, in Experiment 1, we used durations in the infra-second range with a smaller ratio to test the generality of the results in the literature and the claim made by Jozefowiez et al. (2014) that the magnitude of the bias increases as the temporal discrimination becomes harder.

In Experiment 2, we used longer durations with an easier discrimination, and a novel task with location-based responses to observe motion during the sample and compare it to the final choice. Because this variation of the bisection task had not been extensively tested with humans, participants were invited to attend two sessions: the first to learn the task with continous reinforcement and experience a loss in overall reinforcement from 100% per sample to 50%, and the second to experience the differential base-rates (Short-Bias and Long-Bias) with reinforcement set to 50% (thus mantaining overall reinforcement equal to Experiment 1, Chapter IV).

The general scope of the present study was to compare the within-subject effects of differential base-rates on human temporal performance. Importantly, our version of the bisection task aims to bring the study of human timing closer to the domain of non-human animal timing by reducing the number of verbal prompts and studying the learning and perceptual processes in the task.

Experiment 1

Method

Participants. Twelve undergraduate Psychology students (between 18 and 20 years old) of the University of Minho in Portugal participated in the experiment for course credits. At the end of the experiment, the participant with the highest score received a gift card from a local bookstore, valued at 10 euros; participants placed second and third received a note pad. All participants read and signed an Informed Consent Form. Experiments were approved by the University of Minho Ethics Subcommittee for Human and Social Sciences (SECSH 054/2017).

Experimental setting and Stimuli. Experimental setting and stimuli were the same as those described in Experiment 1, Chapter IV.

Procedure. At the beginning of the experiment, participants were given written instructions to listen to the tones and to choose between two keys in the response pad, “S” or “L”, when question marks appeared on the screen. Instructions and pre-training were the same as displayed in Chapter IV, Experiment 1. In pre-training phases, participants learned the short, S (500 ms) and long, L (660 ms) samples. The computer screen displayed “correct” or “incorrect” feedback after each trial, but no points.

Participants were then exposed to three different experimental conditions of a temporal bisection task, as shown on Table 9: Short-Bias (SB), Long-Bias (LB), and No-Bias (NB). Order assignment was randomized, and each possible permutation occurred twice. Each condition was composed of training and test phase, always preceded by a repetition of the pre-training phase.

At the top-center of the screen a counter displayed the cumulative number of points five times during each base-rate condition, after every four blocks, with a short message encouraging the participant to continue trying to get as many points as possible. After each condition, participants took a three-minute break outside the soundproof cabins.

***Base-rate Training*.** Computer instructions informed participants that in this phase they would be able to gain points; however, not every correct response would receive feedback. They were also encouraged to win as many points as possible. This phase introduced the base-rate manipulations (Table 9). In SB, S-trials were more likely to be presented than L-trials. In other words, the proportion of S was 0.75 and the proportion of L was 0.25. In NB, the proportion of trials, was equal for S and L (0.5 – 0.5). In LB, L was more likely to occur than S (0.25 – 0.75).

Table 9

Number of Trials per Block (Short, Long, or Probes) and Corresponding Base-rates per Phase in Experiment 1

Condition	Phase	Trials			Base-rate		
		S	L	Probes	*s*	*l*	Δ
	Pre-training	5	5	0	.50	.50	.0
LB	Training Test	10	30	0 6	.25	.75	-.50
NB	Training Test	20	20	0 6	.50	.50	.00
SB	Training Test	30	10	0 6	.75	.25	+.50

The Base-rate Training phase contained 60 trials, which were randomized in blocks of 10 (5 S and 5 L). The probability of reinforcement, or payoff, was maintained equal for short and long durations in all conditions (.5 – .5). Sample presentation remained as in pre-training but feedback for correct responses, when displayed, was "+ 1 point" shown on the computer screen. Non-reinforced trials and incorrect responses produced a one-second blank screen, followed by the one-second-on-average ITI.

There was no indication for the participants that the training phase ended and the test phase started so as to introduce the test-interval samples inconspicuously between S and L trials.

Base-rate Test. This phase introduced three non-reinforced probe trials – 540, 580, and 620 ms – to each block. Inserting probes maintained reinforcement for the anchors at 0.5 and only reduced the overall probability of feedback in the test phase compared to the training phase to 0.41. The test phase had 12 blocks and a total of 156 trials. Each block consisted of a randomized presentation of five S, five L, and three intermediate trials (one per intermediate duration).

Data analysis. Data analysis was conducted as Chapter IV, Experiment 1. We fitted a cumulative normal distribution with four free parameters, α, β, μ, and σ (Equation 1) to each participant's psychometric function by the method of least-squares (see best-fitting parameters per participant in Appendix J). We conducted repeated-measures analyses of variance (ANOVA), with Condition and Duration as factors, for the psychometric functions as well as for the parameters of the fitted functions. The Greenhouse-Geisser correction was used whenever the sphericity assumption was not met. Differences in means were tested with paired-samples t-tests. We considered a significance level of .05 for all statistical analyses.

Results and Discussion

In pre-training, the participants went through 24.6 (*SEM* = 2.7) trials, on average, and made 4.1 (± 0.7) errors, before moving on to payoff training.

Figure 38 shows the average proportion of correct responses for the Short (S = 500 ms) and Long (L = 660 ms) samples obtained in Base-rate Training. There is an effect of condition: Correct responses for S trials are low when S-trials are more frequent, and increase as the proportion of S-trials decrease. A repeated-measures ANOVA confirms significant effects of condition for the S-trials, $F(2, 22) = 5.27$, $p = .013$, $\eta_p^2 = .32$. Although the figure shows a reverse trend for L, i.e., accuracy decreases as proportion of L increases, it did not reach significance, $F(1.29, 14.21) = 4.088$, $p = .05$, $\eta_p^2 = .27$. Humans tend to expect distributions of S and L samples to be balanced, and try to distribute responses their responses equally (Kutzner, Freytag, Vogel, & Fiedler, 2008). There is evidence that humans tend to neglect base-rates in matching to sample tasks, especially when stimuli are physically similar (Goodie & Fantino, 1996, 1999).

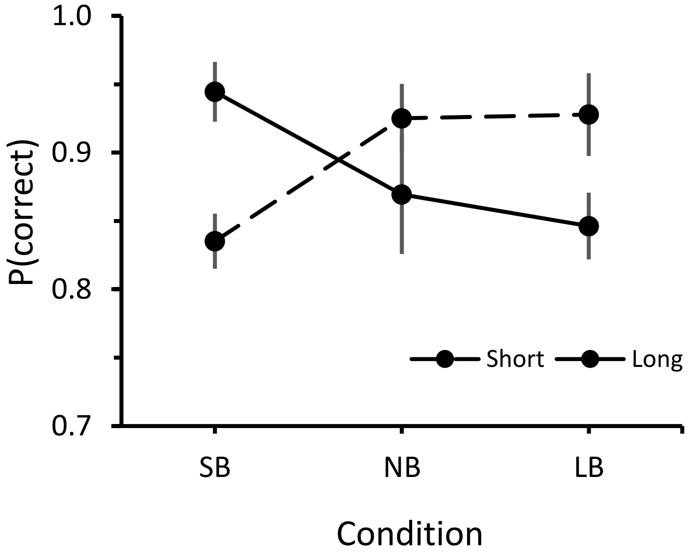

Figure 38. Proportion of correct responses for Long (solid line) and Short (dashed line) samples (*M* ± *SEM*) during the Training phase of each condition in Experiment 1.

Results from the Base-rate Tests are plotted as averaged psychometric functions per condition, and their corresponding fitted Gaussian curves (Figure 39, top panel). The sygmoidal shape of the psychometric functions shows that participants were overall sensitive to the range of durations, $F(2.26, 24.83) = 128.71$, $p < .001$, $\eta_p^2 = .92$. However, the discrimination of the trained samples were not always good, with proportion of "long" choices for S as high as .35 (*Min* = .00) and for L as low as .55 (*Max* = 1.00). Importantly, the functions for the different conditions are not significantly different, $F(2, 22) = 1.35$, $p = .28$.

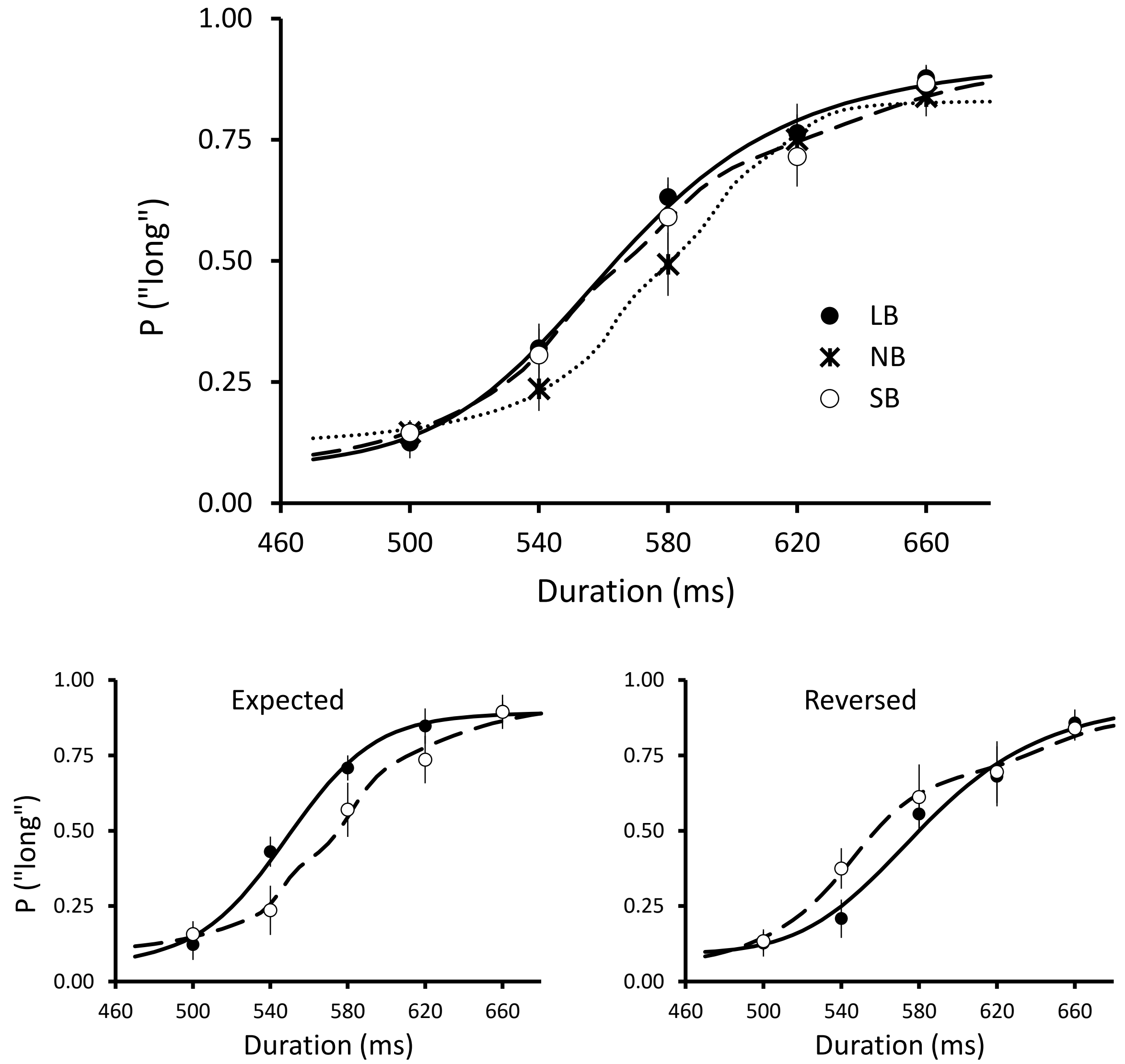

Figure 39. Average proportion of "long" responses (*M* ± *SEM*) per sample duration (symbols) and average of individually fitted cumulative Gaussians (lines) for each condition in Experiment 1: LB (filled circles, solid line), NB (asterisks, dotted line), SB (empty circles, dashed line). Bottom-left: Data from participants producing an expected shift between SB and LB conditions. Bottom-right: Data from participants producing a reversed from expected shift between SB and LB.

Statistical analysis of the fitted parameters revealed that only σ showed a significant effect of condition, $F(2, 22) = 4.42$, $p = .02$, $\eta_p^2 = .287$. However, visual inspection of the individual data showed that participants produced different patterns of responding in the task when comparing the biasing conditions, i.e., with the most extreme Δ values (±0.5).

Statistical analyses confirmed that, while half of the participants produced a higher PSE (μ) for SB than LB, $t(5) = 3.96$, $p = .01$, $d = 1.62$, as expected by timing models such as LeT (and some versions of SET), others showed the reverse (SB < LB), $t(5) = 3.35$, $p = .01$, $d = 1.37$. The “expected” pattern (Figure 39, bottom-left) has been shown by Jozefowiez et al. (2014) with humans, and others (Akdoğan & Balcı, 2016a; Balcı & Simen, 2016) with mice. It has also been found with payoff manipulations (Akdoğan & Balcı, 2016b), but is not always a robust finding in the bisection task (see Galtress & Kirkpatrick, 2010). The bottom-right panel of Figure 39 shows data from participants showing the “reversed” pattern.

Separate analyses of the parameters for the “expected” and the “reversed” group of participants are shown in Figure *40*. Parameters α (top left) and β (top right) determine the minimum and maximum, respectively, and the closer they are to 0, the better the discrimination. While α for the “expected” group shows worse discrimination for NB, with a small effect of condition, $F(2, 10) = 3.67$, $p = .04$, $\eta_p^2 = .25$, there is no effect in the “reverse” group, $F(1, 12.36) = .31$, $p = .62$. Parameter β is unaffected by condition, for both the “expected”, $F(1.20, 13.23) = 0.85$, $p = .40$, and “reversed” groups, $F(1.22, 13.42) = 1.08$, $p = .33$.

For the location parameter, μ (bottom left), which is the halfway point between the maximum and minimum, or PSE, the groups are affected differentially by LB. While “expected” has a significant effect of condition, $F(2, 10) = 6.45$, $p = .02$, $\eta_p^2 = .56$, this is not the case for “reversed”, $F(2, 10) = 2.60$, $p = .12$. While condition NB affects the groups differently regarding the scale parameter, σ (bottom right), neither group shows a significant effect of condition (Expected: $F(2, 10) = 3.73$, $p = .06$; Reversed: $F(2, 10) = 1.37$, $p = .30$).

The standard analysis of averaging the psychometric function for all participants masked an effect of differential base-rates on human performance. While half of the participants showed biasing effects of differential base-rates in the expected direction according to timing theories, i.e., shorter PSEs when L-trials are most frequent. The other half was also affected by the manipulation, but in the opposite direction, i.e., longer PSEs for more L-trials. Although this “reversal” is not readily explained by these theories, it is not unheard of (Daniels, Fox, et al., 2015), and it is possible that manipulating base-rates affects processes that are not time-dependant.

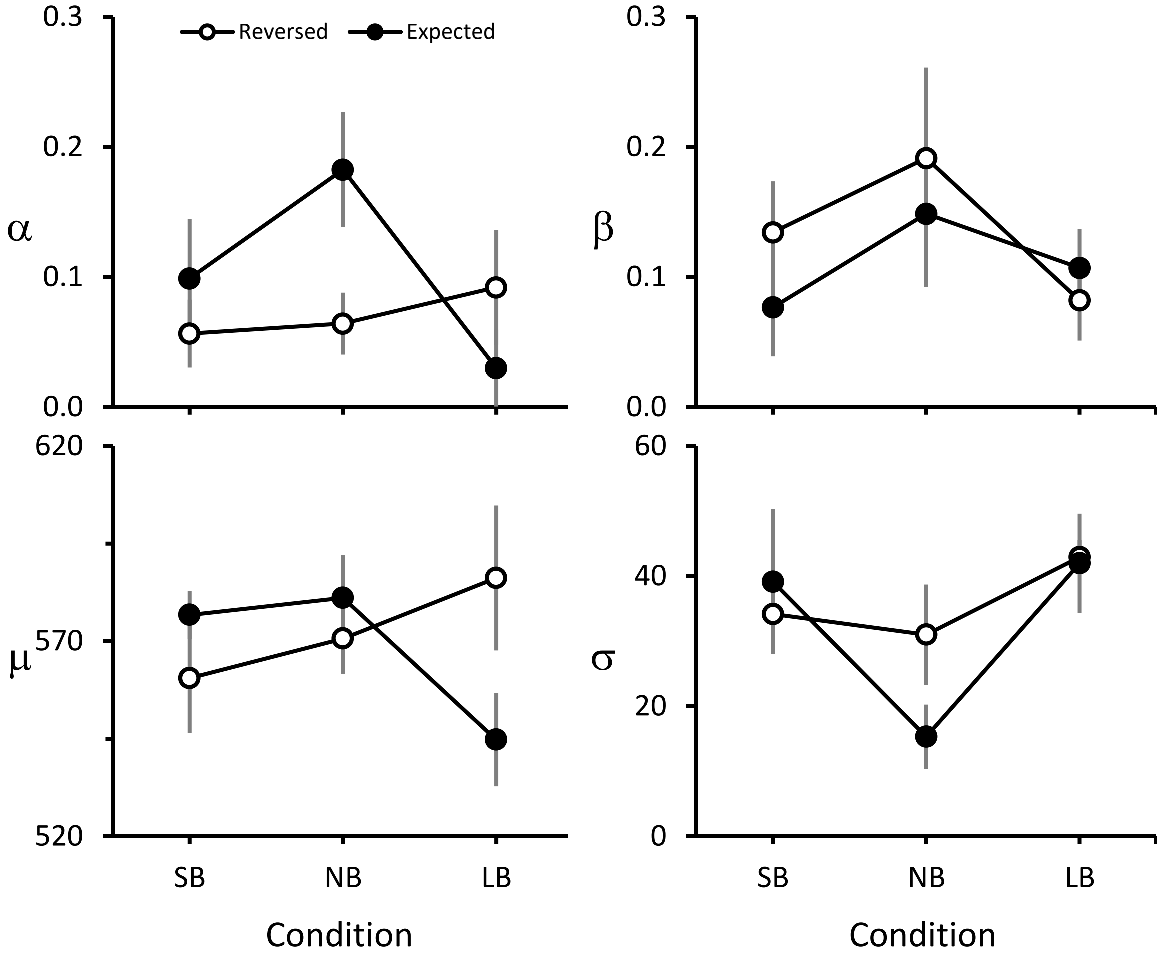

Figure 40. Best-fitting parameters (*M* ± *SEM*) per condition in Experiment 1.

Experiment 2

In Experiment 1, the base-rate manipulations affected the μ parameter, biasing the participants perception of time. However, while half of the participants shifted responding leftward when long trials were more likely, the other half shifted rightward under the same condition. In Experiment 2, we use a location-based mapping to observe motion patterns during the sample and relate to final choice. This may help further our undestading on ongoing decisions regarding the samples made before the choice responses after sample offset. Additionally, anchor durations were increased to provide enough time to record the motion patterns.

Method

Participants. Six undergraduate Psychology students (between 19 and 23 years old) at the University of Minho in Portugal participated in the experiment for course credits. At the end of the experiment, the participant with the highest score received a gift card from a local bookstore, valued at 10 euros. All participants read and signed the Informed Consent

Form. This experiment was approved by the University of Minho Ethics Subcommittee for Human and Social Sciences (SECSH 054/2017).

Experimental setting. Experimental setting was as described in Chapter IV, Experiment 2.

Stimuli. Stimuli used in the computer task were free sound clips downloaded from soundbible.com in WAV format (Appendix I). Sample to-be-timed sound clips were cut using Audacity© software to fit the arithmetic series: 1 s, 1.6 s, 2.2 s, 2.8 s, 3.4 s. Thus, 1 s was the short duration (S), and 3.4 s was the long duration (L). Durations were longer than Experiment 1 so that participants would have enough time to horizontally displace the manipulandum on the screen during the sample.

Procedure. Each participant went through two experimental sessions.

Table 10 shows experimental conditions and phases for each session. Except for condition CRF, which provided 100% reinforcement for anchor, given a correct response, all other conditions had payoffs set at 50% per anchor. Conditions in Session 2 are labelled according to their base-rates for short (*s*) and long (*l*) samples: NB (.5-.5), SB (.75-.25), and LB (.25-.75). Each condition consisted of a training and a test phase. Conditions and phases are presented in order of exposure, except LB and SB, which were counterbalanced.

Table 10

Number of Trials per Block (Short, Long, or Probes) and Corresponding Base-rates per Phase in Sessions 1 and 2 of Experiment 2

Condition	Phase	Trials			Base-rate		
		S	L	Probes	*s*	*l*	Δ
				Session 1			
CRF	Pre-training	6	6	0	.50	.50	.00
	Training						
	Test			3			
NB	Training	4	4	0	.50	.50	.00
	Test			3			
				Session 2			
NB	Training	4	4	0	.50	.50	.00
LB	Training	2	6	0	.25	.75	-.50
	Test			3			
SB	Training	6	2	0	.75	.25	+.50
	Test			3			

Except for the experimental conditions in Session 2, which manipulated the trial base-rates, the remanining details were as specified for Chapter IV, Experiment 2. In fact, Session 1 used the same program for every participant, which was randomly assigned to an experiment and order of conditions in the second session.

Session 2 had six phases: NB Training, SB Training, SB Test, NB Training, LB Training, LB Test. Conditions LB and SB were counterbalanced, so that half of the participants went though LB first and the other half went through SB first.

Results and Discussion

In pre-training, the participants (i.e., all three conditions) went through 26 trials on average (±*SEM* = 5.7), in a minimum of one block and a maximum of three, and made 7.8 (± 3.1) errors. In CRF training, participants went through a maximum of 5 blocks, averaging 36 ± 6.2 trials, and missed 22.6 (± 3.5)% of the trials, i.e., did not respond within the limited hold.

Figure 41 shows the proportion of correct short (S) and long (L) samples during the training phases of conditions Short-Bias (SB), No-Bias (NB), and Long-Bias (LB). While participants were correct on almost 100% of the L training trials, there was a small reduction in the proportion of correct S in conditions SB and NB. Because the short duration is contained within the long one, participants tend to wait for the short duration to elapse before initiating the motion towards their choice. Consequently, on a few trials they will not arrive at the *short* side with enough time to make that choice (i.e., kill the “short” alien).

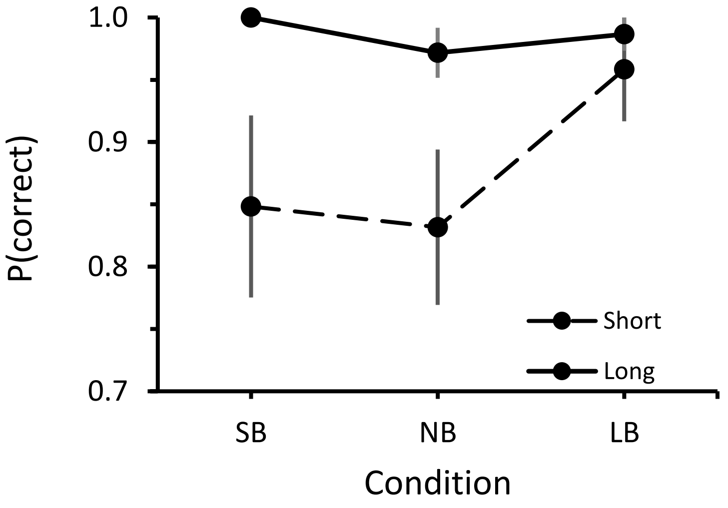

Figure 41. Proportion of correct responses for Short (empty circles) and Long (filled circles) samples (*M* ± *SEM*) during the Training phase of each condition in Experiment 2.

P(“long”). The psychometric functions (and their corresponding fits) from the test phases of each session and condition are shown in Figure 42. In Session 1 (top panel), participants were all exposed to the temporal bisection task with continuous reinforcement (CRF) before reducing reinforcement to 50% per sample (NB). CRF and NB both have sigmoidal shapes. A repeated measures ANOVA confirmed an effect of duration, *F*(1.28, 6.42) = 68.72, $p < .001$, $\eta_p^2 = .93$, but there is no significant effect of condition, *F*(1, 5) = 1.74, $p = .24$, or interaction, *F*(1.58, 7.89) = 4.62, $p = .05$. In Session 2 (bottom panel) conditions SB and LB (bottom panel) also have a significant effect of duration, *F*(1.13, 5.63) = 127.24, $p < .001$, $\eta_p^2 = 0.96$, meaning participants were sensitive to the sample durations. However, these biasing conditions did not affect the psychometric functions significantly, *F*(1, 5) = 1.34, $p = .21$, and there was no significant interaction *F*(1.19, 5.93) = 0.63, $p = .49$.

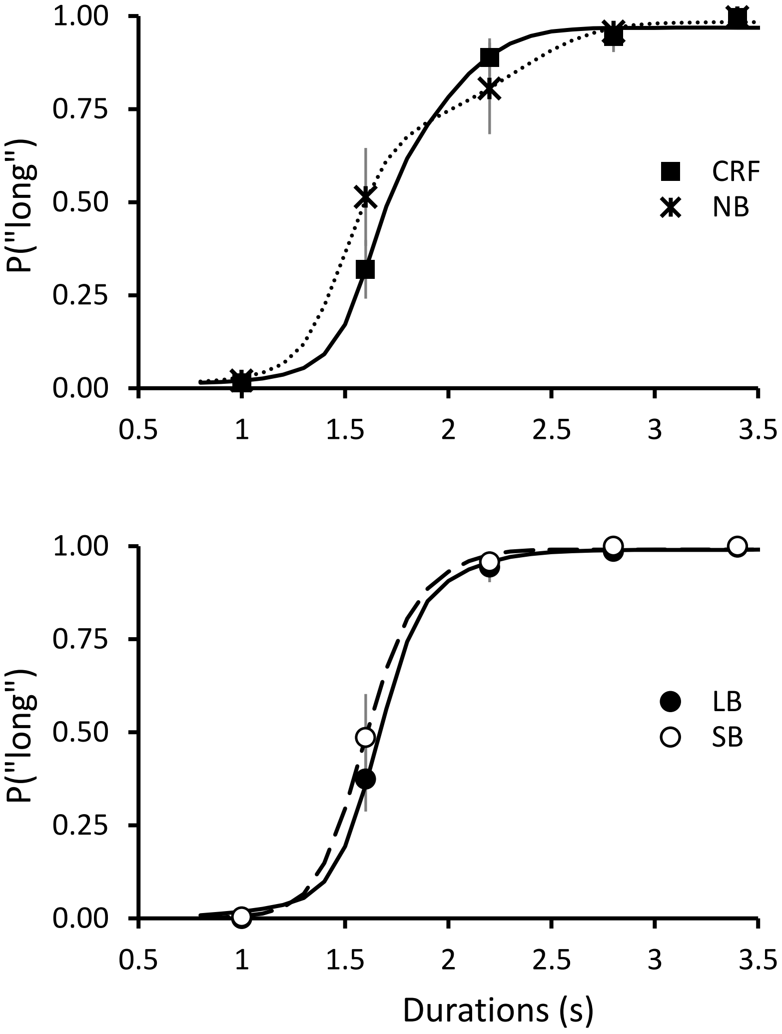

Figure 42. Proportion of “long” responses (*M* ± *SEM*) per sample duration (symbols) and average of individually fitted cumulative Gaussians (lines) for each condition in Experiment 2. Top: Session 1 – CRF (filled squares, solid line) and NB (asterisks, dotted line). Bottom: Session 2 – LB (filled circles, solid line) and SB (empty circles, dashed line).

Discrimination for the anchors was very good in all conditions, as seen by the close to zero minimum (α, top left) and maximum (β, top right) parameters (Figure 43). Although Figure 42 may suggest that function SB is to the left of LB, a parameter analysis indicates no significant effect of condition on the location parameter, μ, *F*(3, 15) = 0.59, *p* = .63 (Figure 43, bottom left). There is also no significant effect of condition on the scale parameter, σ (bottom right), *F*(3, 15) = 0.72, *p* = .56.

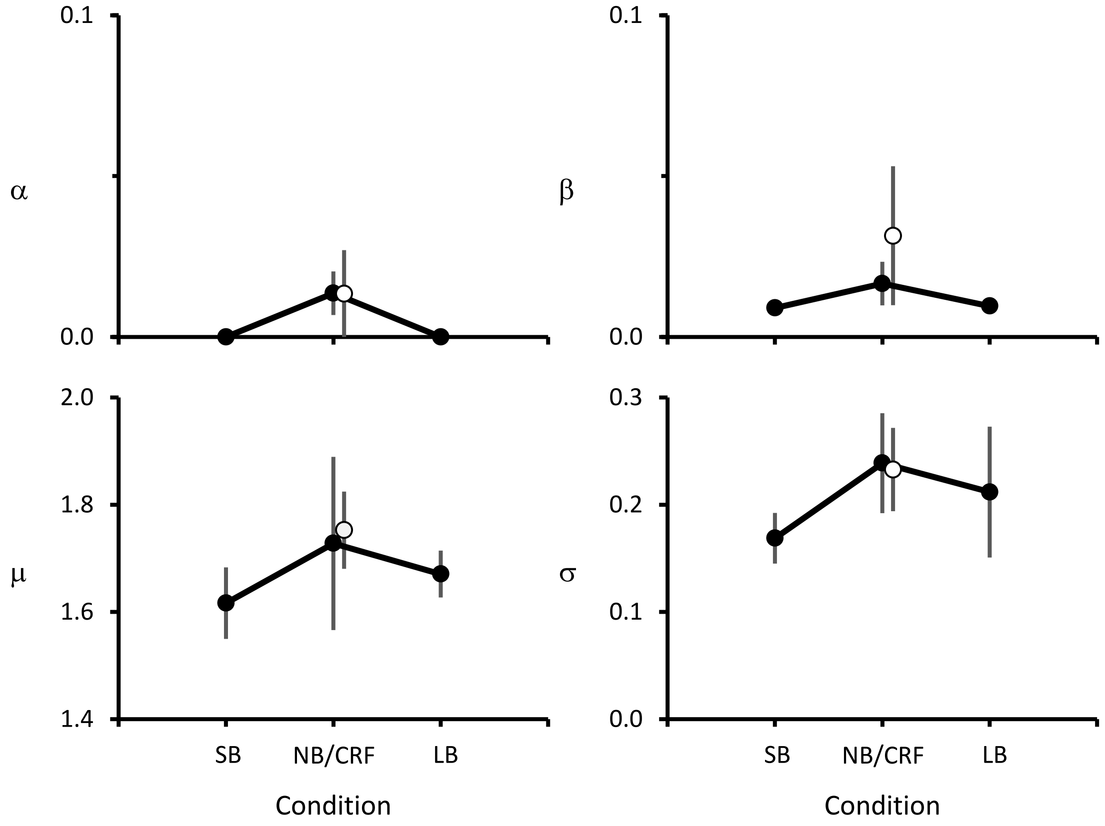

Figure 43. Best-fitting parameters (*M* ± *SEM*) per condition in Experiment 2. Empty circle represents CRF.

Unlike Experiment 1, there is no evidence that the experimental conditions affected the choices made after sample offset – the average psychometric functions are representative of individual functions and parameters (Appendix K, Table K1). This could be attributed to a number of factors individually or conjointly, such as the ratio of the durations, the spacing of the probes (Wearden & Ferrara, 1995), insensitivity to the probabilities due to the small differential values (±0.5), or due to the stereotypical patterns leading to self-generated rules

(Baumann et al., 2017), ignoring instructions, or counting behavior (Daniels, Fox, et al., 2015; Rakitin et al., 1998).

Motion Patterns. Figure 44 shows the motion patterns during L-samples for the first block of pretraining (left), the first block of training (center), and the last block of training (right), for a representative participant. From left to right, the panels show how the participant learned to move during the sample. Initially, participants tend to stay around the center for about 2 s, and after moving they do not necessarily go to the correct side, i.e., $\lambda(t) = 6$. Then, a more clear pattern began to emerge, where they tended to remain at the center until the short duration had elapsed, then move to the *long* side, arriving before the long sample had elapsed. Finally, all participants learned to move to the *short* side (Arrival Time - AT), wait a few seconds (Residence Time - RT), then move to the *long* side (Departure Time - DT). With a limited hold (0.5 s), shorter than described in Chapter IV, Experiment 2, participants had to start moving almost immediately to arrive and shoot at the *short* side and avoid being killed by the aliens. In the last block of training, average AT = 1.48 s (± 0.3), RT = 0.52 s (± 0.05), and DT = 1.72 s (± 0.03).

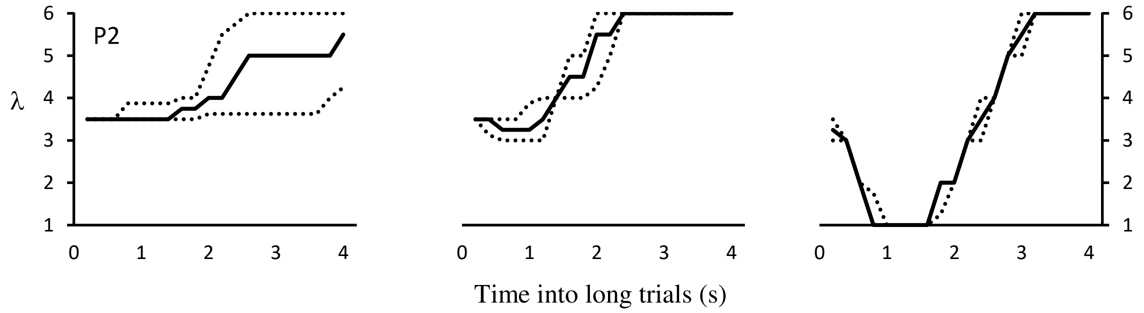

Figure 44. Motion patterns for representative individual (P2) during long sample trials for pre-training and CRF training in Experiment 2. Left – first block of pre-training; center – first block of training; right – last block of training. Median = solid line; quartiles = dotted lines.

The individual median motion patterns produced in the base-rate test phase of conditions LB and SB are depicted in

Figure *45*. Three participants maintained the *short-long* pattern for both conditions, despite the increase of the limited hold during testing. Four participants (P1, P2, P3, and P5) departed to *long* about earlier when the L trials were most likely, condition LB, compared to SB, when S-trials were most likely. P4 and P6 showed no difference in motion parameters AT, RT, or DT. On average, AT = 1.40 s (± 0.02) and RT = 0.43 s (± 0.04) for condition LB and AT = 1.64 s (± 0.03) and RT = 0.32 s (± 0.04) for condition SB. While four departed earlier when “long” produced higher payoffs, two departed later, with average DT = 1.92 s (± 0.05) in LB and 2.06 s (± 0.08) in SB, *t*(5) = 2.02, p = .01.

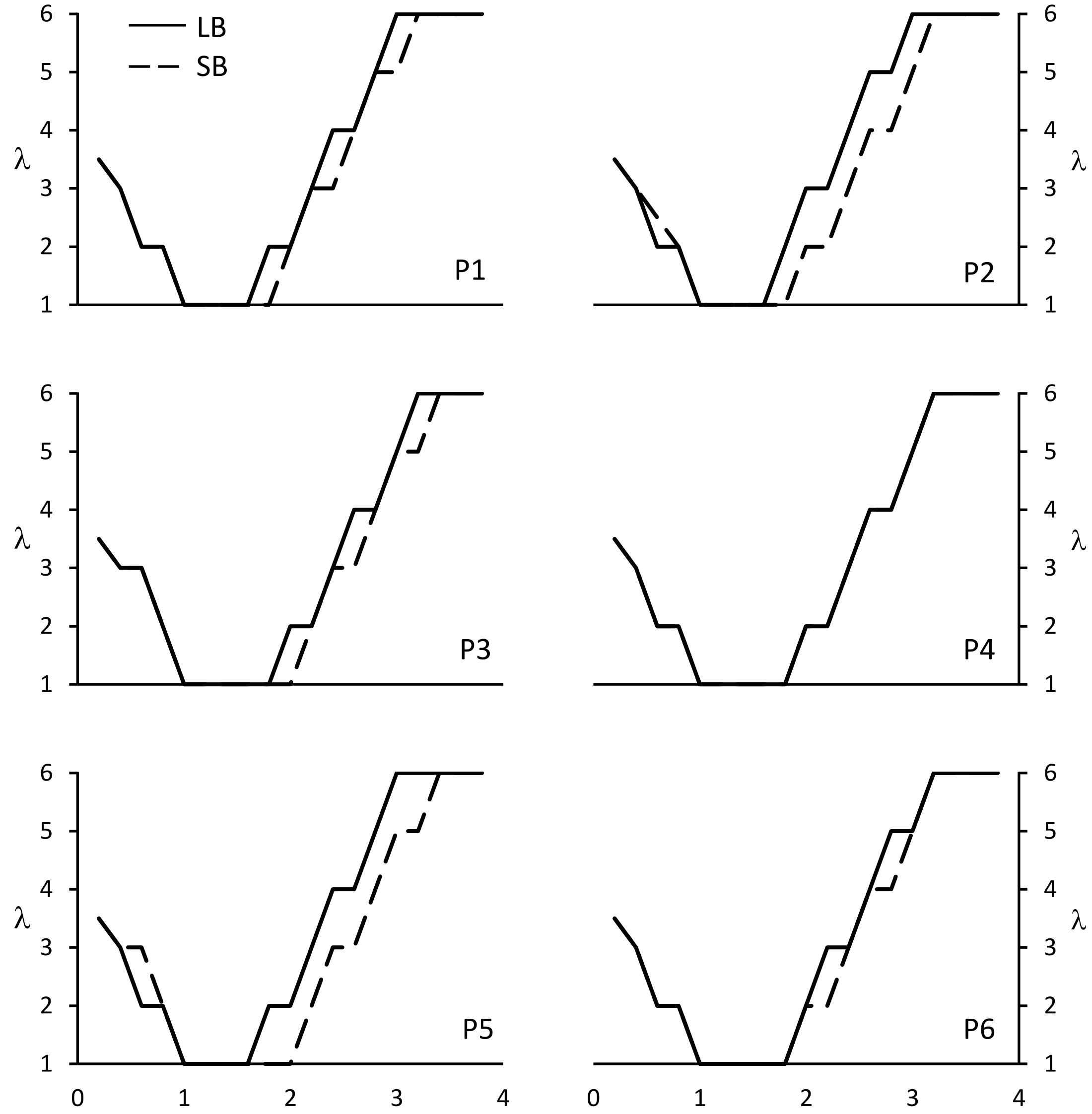

Figure 45. Motion patterns (median only) during long sample trials for conditions SB (dashed lines) and LB (sold lines) tests in Experiment 2.

Departure times and P(“long”). The moment the spaceship departs toward the *long* side may be considered a measure of indifference between short and long durations in the bisection task, analogous to the PSE, and the empirical cumulative distribution of departure times (DT) equivalent to the psychometric function (Machado & Keen, 2003). Figure 46*Figure 37* compares the average psychometric functions per condition to their corresponding distribution of DTs. The top figure shows that, despite there being no difference between psychometric functions in the differential base-rate tests, the distribution of departure times for SB is to the right of LB, corroborating the data from Figure 45. This indicates that motion patterns were affected by the experimental conditions, with participants departing later when S-trials were most likely.

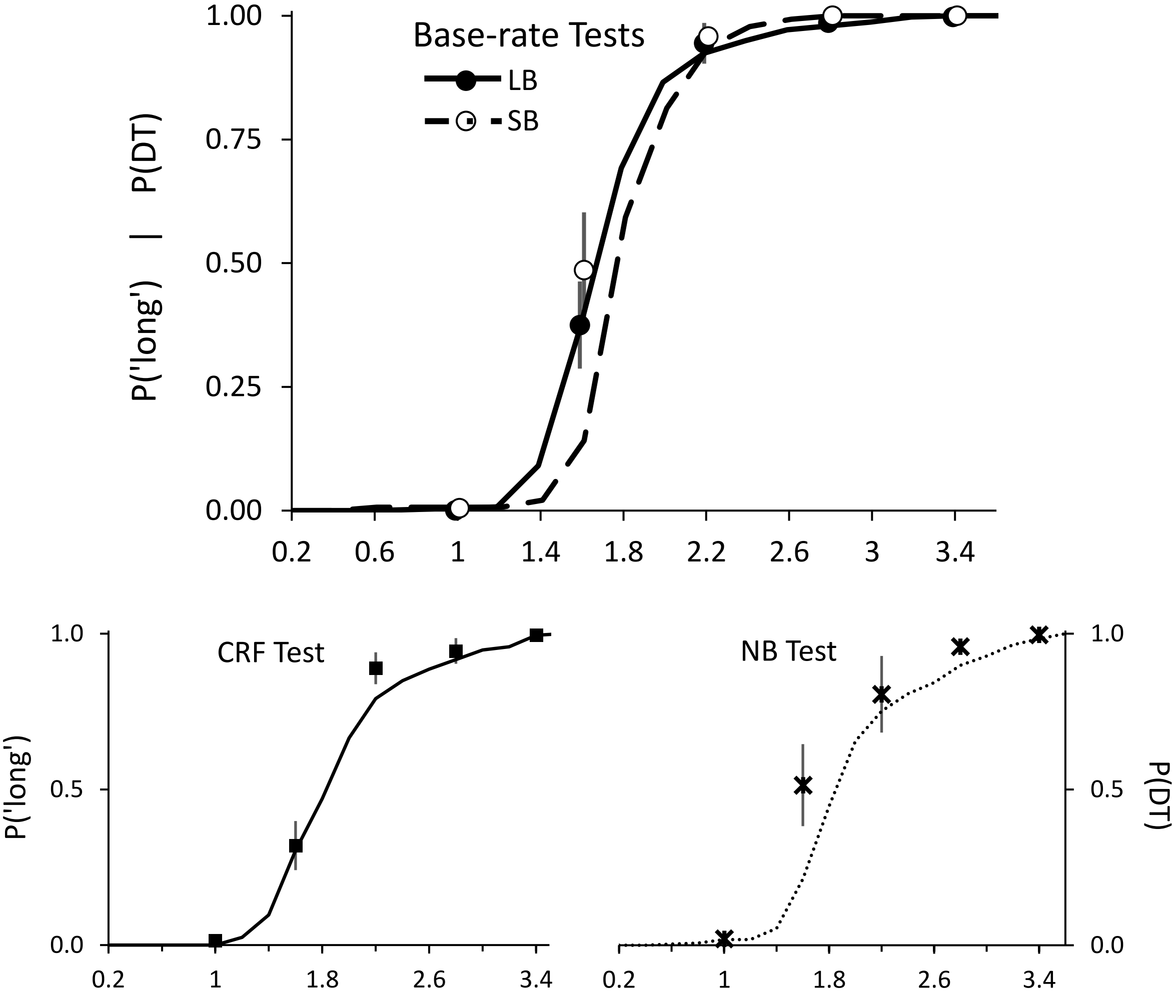

Figure 46. Averaged empirical cumulative distribution function of departure times (lines) plotted against proportion of "long" (symbols). Top: LB (solid line, filled circles) and SB (dashed line, empty circles); Bottom-left: CRF; Bottom-right: NB.

While conditions LB (top) and CRF (bottom-left graph) show a very good approximation between the distribution of DTs and the proportion of "long" (individual data is presented in Table K2, Appendix K), SB (top) and NB (bottom-right) show a mismatch between these measures, particularly for the 1.6 s sample. This indicates that, on those trials, participants only departed after sample offset. This is likely a combination of departures from the *short* side very soon after sample offset and the low resolution of location points (150 pixels apart). In CRF and SB, departures are a little bit earlier than sample offset. Future studies should program more sensitive measures of motion to avoid this type of mismatch. A dissociation between final choice and motion pattern has been previously reported in humans (Chapter V) and pigeons (Chapters II and III). However, in those cases, p("long") was smaller than cumulative departures because the subjects were "breaking" the stereotypical *short-long* pattern and returning to the short side after sample offset.

This experiment replicates with human participants results from Machado and Keen (2003). As their pigeons, most of our participants learned to move to the *short* side at sample onset, wait for the S interval, then depart to *long.* Also, departure time (DT) was generally a good estimate of the PSE. Earlier departure times for Long-Bias also replicate findings from a similar procedure with humans using a differential payoff manipulation (Chapter IV), as well as payoff (Chapter II) and base-rate (Chapter III) data from pigeons.

General Discussion

The purpose of the present study was to see how differential trial base-rates affected responding in a temporal bisection task. In Experiment 1, participants went through a typical bisection task, learning a duration-key association (e.g., short—"S", long—"L"), before being exposed to three experimental conditions. Experiment 2 extended previous studies to a duration—location association (e.g., short—"left", long—"right"), with response locations far apart to enable recording motion patterns during the sample intervals. To measure the effects of varying the base-rate differential, we computed psychometric functions and estimated their location and scale parameters, measures of response bias and temporal sensitivity, respectively; as well as the upper and lower asympototes, measures of discrimination of the trained samples. In Experiment 2, we also computed the distributions of departure times (DT) to relate the motion patterns during the sample to choice behavior after the sample.

We evaluated the robustness of the findings reported with humans (Balcı & Simen, 2016; Jozefowiez et al., 2014) and rats (Akdoğan & Balcı, 2016a) in which the subjects tend to bias responding towards the key associated with the sample duration presented most often. The authors of these studies indicated that these biases were relatively small (some models predict almost exclusive preference, i.e., large shifts; see Jozefowiez et al., 2014) and nearly optimal (Akdoğan & Balcı, 2016a; Çoşkun et al., 2015). Jozefowiez et al. (2014) also suggested that the magnitude of the bias may be affected by the difficulty of the discrimination. Experiment 2 did not produce consistent shifts in psychometric functions with an easier discrimination (1:3.4 s), such as a previous study with mice manipulating magnitude of reinforcers with a duration ratio of 1:4 s (Galtress & Kirkpatrick, 2010).

On the other hand, Experiment 1, with a duration ratio of 1:1.2, should have produced equal or greater shifts compared to previous studies using a ratio of 1:1.5. Although the average results did not show evidence of response bias, the small sample size enabled us to observe individual trends. While half of the participants in Experiment 1 produced a leftward shift in LB, i.e., bias for "long" choices, the other half showed the opposite response pattern. While this reversal may be difficult to explain, it has been previously reported with humans (Daniels, Fox, et al., 2015). Although this phenomenon could be attributed to peculiarities in the way humans track time (Allan, 1998), our current preparation does eliminate some hypotheses presented by Daniels, Fox, et al. (2015), such as practice effects, since our order of conditions was counterbalanced, or counting, since our durations were very short and reasonably difficult to discriminate.

Typically, human and non-human animals learn a duration—key association, such as the preparation from Experiment 1. In Experiment 2, presenting a duration—location association enabled us to observe timing behavior during the samples and reveal a dissociation between the distribution of departure times and final choice. While there is no evidence of p("long") being affected by the base-rates, four out of six participants shifted their departure times, leaving earlier for more L-samples than when there were more S-samples.

The present study showed that control of temporal behavior may be affected by differences in the relative frequencies of short and long sample stimuli in a bisection task, although effects were not robust. Integrating the information from these experiments will contribute to our understanding of the basic process of interval timing and learning. However, our findings suggest strong methodological recommendations. Further investigation will enable us to understand and mathematically define the specific role of variables such as the ratio or probability differential of the trained trial base-rates, their discriminability, and the relation between the training and test settings in the temporal bisection task.

CHAPTER VI

CONCLUSIONS

In the present dissertation, we evaluated the robustness of previous findings on the effects of differential payoff and base-rate manipulations on temporal discrimination of two species: *Columbia livia* and *Homo sapiens*. Our major goal was to further our understanding about the role these non-temporal variables play in the timing process. Subjects went through two versions of the temporal bisection task: the standard task, where they learned the association between two durations and arbitrary keys, and a novel task, where they learned the association between two durations and response locations. In the novel task, we recorded motion patterns from sample onset and related them to choice after sample offset. In a sense, we wished to observe ongoing timing during the bisection task, thus bringing it closer to other procedures that measure response rate during a to-be-timed interval.

Throughout a series of parametric experiments, we tested three conditions: Long-Bias (favoring the long sample or response), Short-Bias (favoring the short sample or response), and No-Bias (with equal sample and reinforcer probabilities). We observed acquisition of the temporal discrimination and evaluated the psychometric function (i.e., the proportion of "long" choice at the end of intermediate sample durations), notably for response bias and sensitivity to the intervals. Although systematic variation in either sample frequency or associated reinforcement probabilities showed no indication of changes in sensitivity, we found consistent evidence of response bias, especially for pigeons. This is consonant with previous data in the literature and timing models; however, the effect was smaller than observed in similar research using other preparations – possibly, the magnitude of the shifts is positively correlated to the sample durations.

Standard *vs*. Novel Task

In each chapter, we first used the standard bisection task and then replicated some experimental conditions with the novel version of the task. Motion patterns produced during acquisition of the location-based novel task replicated those found in Machado and Keen (2003): For long samples, subjects moved toward the *short* side at sample onset, remained for a few seconds, then departed toward the *long* side. This was also true for human participants, but only once a limited hold to respond immediately after sample offset was implemented, to motivate motion during, instead of after, the sample.

Psychometric functions for both tasks tended to follow the typical sigmoidal shape. Visual inspection showed that subjects tended to have better discrimination of the trained samples in the novel task. Because this task had longer interval samples, the subjects had plenty of time to arrive at the *short* side before the short sample elapsed, wait, and still arrive at the *long* side well before the long sample elapsed. Thus, not only was the discrimination between the trained samples easier due to their ratio but developing stereotypical motion patterns induced by the location-based associations meant that subjects could also use their own location as a cue to respond.

Other preparations have also found that temporal discrimination was enhanced when animals were required to “fill” a duration with behavior than when there was no such requirement (Harper & Bizo, 2000). Our variation required subjects to be at a specific location to respond, thus, motion patterns could be considered a mediating behavior (Ferster & Skinner, 1957) that may have contributed to the accurate learning of the sample-response mappings.

Finally, analyzing motion patterns during experimental conditions brought about unexpected but compelling results – a dissociation between the distribution of departure times and the psychometric function. Because the dissociation was not the same between species or manipulations, it will be discussed further in the following sections.

Payoff *vs*. Base-rate Manipulations

In Chapters II and IV we manipulated payoffs and in Chapters III and V, base-rates. Results from Chapter II indicated that to better understand the effects of differential payoff we should probably consider the role of overall changes in reinforcement between conditions. Although this is worthy of further investigation, for our current purposes, we used this information to improve our control of this possibly confounding variable in the subsequent experiments.

Another interesting issue that arose is the probabilistic nature of the variables presented in the experiment. Although some manipulations tend to be treated as equal or similar, and thus sometimes categorized as “motivational” (e.g., deprivation levels, magnitude of reinforcement, probability of reinforcement), this may not be the case. It is likely that magnitude manipulations affect timing differently than rate or probabilities of reinforcement. It is also conceivable that variables sometimes thought to be different are functionally similar – such as the evidence for payoff and base-rate.

However, the payoff manipulations seemed to have a more robust effect on temporal discrimination than base-rate manipulations, especially concerning human subjects. One possibility may be related to the fact that participants exposed to unequal base-rate conditions tend to be more optimal in their decision making than those exposed to unequal payoffs (for a review, see Maddox, 2002). Because biasing may be interpreted as a deviation from optimality, one could surmise that base-rates would lead to lesser deviations from baseline in interval timing as well.

Lastly, unlike Machado and Keen (2003), we observed that, in some conditions, pigeon's distribution of departure times did not match the proportion of "long" key choices for the intermediate samples, especially at the geometric mean of the short and long durations – the moment when they were most likely to be around the center of the chamber (after having arrived and departed from the *short* side). Additional analyses showed that choice was correlated with the location of the animal in the chamber at sample offset: the closer to the short side, the higher the probability of returning to choose "short" after having departed towards long. This interacted with the experimental manipulations in interesting ways. In the payoff experiment, this disruption in the stereotypical short—long motion pattern occurred mainly during Long-Bias and Short-Bias, which could indicate an overall loss of temporal control that was superseded by spatial control at sample offset. In the base-rate experiment, pigeons surprisingly mismatched from baseline, which could relate to generally lower deprivation levels.

Pigeon *vs*. Human Subjects

In Chapters II and III we conducted the experiments with pigeons, while Chapters IV and V replicated the experiments with human participants. In general, humans showed worse discrimination of the trained samples in the standard bisection task, most likely because the ratio was much smaller, and thus we fitted a four parameter Gaussian-like distribution to human performance, and a two-parameter distribution for pigeons. Otherwise, performance in both versions of the task during baseline conditions was comparable.

Performance during biasing conditions, however, showed some differences between species. Namely, the payoff manipulations produced overall differences in proportion of "long" choices for humans, but only significantly affected the mean parameter (bias) in the novel version of the bisection task. The base-rate manipulations were even less consistent, with only half of the participants producing a bias in the standard task, while the other half produced a "reversal" that cannot be explained by timing theories alone. This case speaks for the importance of considering individual data to avoid averaging artifacts.

Nonetheless, it is too early to determine whether differences are species-specific because, despite the adjustments made for the task with human participants, there are still many distinctions between the procedures used with humans and those used with pigeons. One important concern is the length of exposure to the experimental contingencies. While non-human animals engage in the task for months, and each condition for many sessions, college students are seldom willing to participate in more than two sessions.

Because in the current dissertation we were interested in the effect of training in temporal performance, reinforcers are particularly important. One general issue in comparative psychology pertains to the nature of stimuli used as reinforcers, or the differences in motivational context: While we typically use primary reinforcers with pigeons (food), human participants only receive arbitrary points during the task. We tried to resolve this in two ways:

1) Since we could not afford to pay each participant an amount contingent to their performance, we informed them that the best performances would receive a gift card. However, not having access to the scores of other participants to compare may have reduced the motivating effect of this instruction.
2) We created a game version of the task. Although this seemed to maintain more interest in the task, having longer sample durations for the novel task still meant that sessions were reasonably long, while not comprising a lot of trials.

Another question relates time of exposure to the task and intermittence of the reinforcers. Perhaps the participants needed longer exposure to the consequences of their responses in the task. While differences in a contingency such as correct "short" response = 1 point and correct "long" = 4 points should be immediately recognizable within a few trials, longer experience with the task is necessary to recognize probabilistic reinforcement and differences in probabilities between two options.

It is also worthy of consideration that while the novel bisection task involves somewhat increased physical effort for pigeons moving along the operant chamber, this is not the case for humans pressing keys in a computer. In baseline conditions, or when overall reinforcement was reduced, some pigeons stopped going all the way to the farthest *short* location; this reduces effort in exchange for a small lag in obtaining food on the short trials (which does not necessarily imply faster access to food on long trials since the birds typically arrive many seconds early). This means that the behavior patterns are not as stereotypical as previously thought (Machado & Keen, 2003).

Finally, it is interesting that human subjects showed a different type of mismatch between the psychometric function and the distribution of departure times as compared to pigeons. Pigeons learned to return to the *short* side, thus breaking the *short-long* motion pattern. While the sample offset was a cue to respond, location in the chamber (interacting with the programmed probabilities) was highly correlated with the choice to "return" to *short* or "keep going" to *long*.

To approximate the task with humans (game) to those with pigeons, there were few instructions so that participants would "figure out" the contingencies as they played. This may have led to self-generated rules (Galizio, 1979), such as "go *short*, shoot; go *long*, shoot", which created highly stereotypical behavior and decreased sensitivity to the sample presentation contingencies. Also, taking long to respond had aversive consequences, meaning participants were less likely to return to the *short* side after having already departed – a movement pattern that has been observed in our pigeon experiments.

Consequently, the payoff and base-rate manipulations tended to affect the departure time more than the final choice in human participants going through the "novel" bisection task. In a sense, this dissonance may reflect differences between response and perceptual bias, since departure times could be considered a more straightforward measure of temporal perception during the interval, while the choice may be primarily rule-governed.

LeT *vs*. SET Models

While our main goal was not to directly contrast timing models, our data does have some interesting implications for their future development. First, as described in the Introduction (Chapter I), while a SET-like model, given some alterations, could predict a bias effect from differential base-rate and payoff manipulations in a temporal bisection task, it predicts almost absolute preference for one of the keys, i.e., very large shifts (see Jozefowiez et al., 2014, for a simulation). This is not consistent with our results showing that payoff and base-rate manipulations biased responding with shifts that were small in magnitude. An associative account of timing, such as LeT's (Learning-to-Time), predicts modest shifts and is thus more likely to be an accurate representation of the timing processes involved in the bias phenomenon.

Moreover, together with previous studies (Meck, 1996) there is some evidence that the easier the discrimination, the smaller the magnitude of the bias (c.f., Experiments I and II, Chapter II). SET's predictions are independent of the durations, while LeT's are not. Other models, such as BEM, will make the same qualitative and quantitative predictions as LeT. Thus, evidence in favor of LeT is evidence for an associative account of the timing process, as opposed to more cognitive accounts.

However, neither of these accounts directly considers competition of control by temporal and non-temporal variables over timing behavior. Modifications, such as proposed by Daniels, Fox, et al. (2015), of incorporating timing and non-timing states in which a subject will enter with some probability at trial onset, are one legitimate direction. However, throughout this dissertation we observed that pigeons tended to begin most trials by timing and the temporally correlated behavior "broke" when the stimulus offset indicated time for choice when the animal was in neither choice location (Chapters II and III). New behavioral models that have emerged trying to consider competition for stimulus control (e.g., Cowie et al., 2014; Cowie, Davison, & Elliffe, 2015) could have a predictive advantage regarding temporal biases.

The challenges faced throughout this project feature how critical it is to do research on interval timing and shed light to seemingly obscure phenomena such as temporal biases and other perceptual and learning processes. This dissertation is an advancement in our understanding of interval timing and its relation to learning, perception and behavior in general. And hopefully a stepping stone for further research and theoretical progress on how human and non-human animals are influenced by the passage of time.

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APPENDICES

Appendix A

Parameters obtained from individual cumulative Gaussian fits of psychometric functions in Experiment 1, Chapter II: Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Table A1

Experiment 1A

Condition	Parameter	P190	P284	P588	P639	P785	P841	Average
Generalization Test	μ	5.84	6.13	5.49	6.71	4.52	6.26	5.83
	σ	1.51	1.46	1.60	3.36	1.50	1.58	1.84
	R^2	.979	.995	.992	.978	.976	.966	.981
LB$_{(0.1\text{-}1.0)}$	μ	5.26	5.24	4.76	5.26	5.94	4.36	5.14
	σ	1.44	2.12	2.19	1.44	2.03	1.00	1.71
	R^2	.911	.963	.973	.627	.959	.993	.904
LB$_{(0.1\text{-}0.5)}$	μ	5.03	3.79	4.21	4.31	2.52	5.03	4.15
	σ	1.94	1.55	1.51	3.65	2.58	0.93	2.03
	R^2	.969	.949	.972	.823	.988	.998	.950
NB$_{(0.5\text{-}0.5)}$	μ	5.68	6.01	5.37	5.81	5.55	5.89	5.72
	σ	1.07	1.24	2.69	2.53	3.74	2.10	2.23
	R^2	.981	1.000	.965	.993	.771	.891	.933
SB$_{(0.5\text{-}0.1)}$	μ	15.27	6.33	8.14	8.86	4.36	9.58	8.76
	σ	9.44	0.76	2.93	3.73	1.75	0.71	3.22
	R^2	.653	.927	.827	.910	.995	1.000	.885
SB$_{(1.0\text{-}0.1)}$	μ	5.37	9.19	10.16	8.08	5.48	10.93	8.20
	σ	1.77	1.96	4.30	2.53	2.43	3.84	2.80
	R^2	.942	.996	.746	.968	.838	.942	.905

Note. Shaded cell indicates outlier.

Table A2

Experiment 1B

Condition	Parameter	P190	P284	P588	P639	P785	P841	Average
LB$_{(0.1\text{-}1.0)}$	μ	4.64	1.79	3.38	5.11	4.99	5.16	4.18
	σ	2.77	3.21	2.83	1.49	1.83	1.30	2.24
	R^2	.997	.921	.905	.996	.997	.977	.966
LB$_{(0.1\text{-}0.5)}$	μ	4.67	3.96	4.41	4.26	3.64	4.94	4.31
	σ	1.78	1.28	1.52	2.64	1.79	1.44	1.74
	R^2	.963	.964	.993	.837	.967	.995	.953
NB$_{(0.5\text{-}0.5)}$	μ	5.94	5.41	6.34	5.90	5.57	4.77	5.65
	σ	1.45	0.97	2.35	1.11	1.05	0.63	1.26
	R^2	.996	.998	.993	.997	.985	.986	.992
SB$_{(0.5\text{-}0.1)}$	μ	5.97	10.23	9.59	7.87	5.80	7.62	7.85
	σ	1.94	4.02	4.23	4.35	1.17	2.40	3.02
	R^2	.989	.941	.996	.959	.989	.997	.978
SB$_{(1.0\text{-}0.1)}$	μ	6.24	6.54	7.52	10.09	5.65	6.08	7.02
	σ	2.02	0.74	2.47	7.12	1.19	1.53	2.51
	R^2	.951	.987	.971	.869	.986	.996	.960

Appendix B

Individual best-fitting parameters in Experiment 2, Chapter II: Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Table B1

Cumulative Gaussian Distribution

Condition	Parameter	P088	P301	P501	P116	P463	P536	Average
$\text{LB}_{(0.2\text{-}0.8)}$	μ	4.58	6.80	5.22	5.41	5.51	5.20	5.45
	σ	0.86	1.45	0.64	0.77	0.83	1.06	0.94
	R^2	1.000	.995	.987	.997	.986	.988	.992
$\text{NB}_{\text{L}(0.5\text{-}0.5)}$	μ	5.10	5.54	5.32	7.76	5.69	5.62	5.84
	σ	0.56	0.37	0.70	0.46	0.40	1.48	0.66
	R^2	1.000	.998	1.000	.998	.993	.989	.996
$\text{SB}_{(0.8\text{-}0.2)}$	μ	5.42	6.53	6.33	7.11	5.75	5.65	6.13
	σ	0.76	1.92	1.41	1.14	0.42	0.41	1.01
	R^2	.939	.957	.992	.995	.998	.987	.978
$\text{NB}_{\text{S}(0.5\text{-}0.5)}$	μ	4.70	5.46	5.10	5.10	5.10	5.10	5.09
	σ	0.32	0.34	0.60	0.57	0.57	0.10	0.42
	R^2	.998	.996	.997	.997	1.000	.997	.998

Table B2

Empirical Cumulative Distribution Function of Departure Times

Condition	Parameter	P088	P301	P501	P116	P463	P536	Average
$\text{LB}_{(0.2\text{-}0.8)}$	*M*	4.64	5.23	4.82	4.93	5.40	1.77	4.46
	SD	1.10	2.54	2.34	1.78	2.36	1.16	1.88
	R^2	.92	.56	.84	.87	.95	.81	.83
$\text{NB}_{\text{L}(0.5\text{-}0.5)}$	*M*	5.04	5.32	5.13	5.23	5.65	5.54	5.32
	SD	1.15	2.56	1.77	2.34	2.43	2.77	2.17
	R^2	.93	.97	.97	.52	1.00	.91	.88
$\text{SB}_{(0.8\text{-}0.2)}$	*M*	5.08	5.96	5.33	5.71	6.03	5.83	5.66
	SD	0.79	2.13	2.42	0.97	2.28	2.29	1.82
	R^2	.87	.85	.75	.57	.99	.99	.84
$\text{NB}_{\text{S}(0.5\text{-}0.5)}$	*M*	4.95	5.61	4.82	5.96	5.72	5.45	5.42
	SD	0.88	2.67	1.58	2.84	1.80	2.63	2.07
	R^2	.96	.99	.89	1.00	1.00	.98	.97

Note. Shaded cell indicates outlier.

Appendix C

Number of “long” Choices/Location at Sample Offset for Each Intermediate Duration in Conditions LB and SB in Experiment 2, Chapter II (Pooled Across Birds)

Location	**LB$_{(0.2-0.8)}$**			**SB$_{(0.8-0.2)}$**		
	4.2 s	**6 s**	**8.5 s**	**4.2 s**	**6 s**	**8.5 s**
1	1/44	0/6	1/1*	0/71	0/10	0/9
2	1/31	0/1*	0/1*	0/29	1/16	0/2
3	4/13	6/12	0/0*	1/5	17/32	0/2
4	1/3	12/16	2/2	0/0*	10/12	2/3
5	2/2	28/36	32/32	0/0*	26/30	33/33
6	4/15	33/37	69/72	0/0*	5/5	56/56

*Note.** Proportions not calculated for locations occuring on fewer than two trials.

Appendix D

Parameters obtained from individual cumulative Gaussian fits of psychometric functions in Experiment 1, Chapter III: Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Table D1

Experiment 1A

Condition	Parameter	P547	P726	P730	P746	P752	P851	P917	Average
Generalization Test	μ	6.11	4.67	5.29	5.99	5.40	5.09	5.58	5.41
	σ	2.28	1.29	1.96	1.72	1.31	1.05	2.51	1.71
	R^2	.992	.990	.960	.996	.994	.966	.976	.982
LB$_{(0.1-0.9)}$	μ	4.93	5.00	3.19	4.09	5.45	3.92	5.52	4.59
	σ	1.89	0.29	3.17	2.82	2.54	1.58	2.37	2.09
	R^2	.989	.968	.922	.864	.968	.854	.986	.936
LB$_{(0.2-0.8)}$	μ	5.26	6.02	4.30	4.44	4.67	4.81	5.84	5.05
	σ	0.33	2.06	1.44	1.29	0.79	0.89	1.43	1.18
	R^2	1.000	.969	.961	.993	.989	1.000	.999	.987
NB$_{(0.5-0.5)}$	μ	6.00	4.83	5.54	4.83	5.90	4.25	5.49	5.26
	σ	1.30	1.50	2.07	0.93	1.32	0.68	2.18	1.43
	R^2	.998	.965	.913	.993	.989	.991	.997	.978
SB$_{(0.8-0.2)}$	μ	5.91	6.20	6.95	5.38	4.78	5.53	9.00	6.25
	σ	1.25	1.69	2.13	2.08	0.62	2.69	1.57	1.72
	R^2	.920	.965	.942	.940	.988	.804	.913	.925
SB$_{(0.9-0.1)}$	μ	6.12	6.68	6.69	5.42	5.06	5.50	6.44	5.99
	σ	1.33	1.64	4.30	0.87	0.32	1.54	0.95	1.56
	R^2	.961	.985	.501	.988	.989	.969	.991	.912

Table D2

Experiment 1B

Condition	Parameter	P547	P726	P730	P746	P752	P851	P917	Average
LB$_{(0.1-9.0)}$	μ	5.08	4.90	4.93	5.31	5.01	5.00	4.84	5.01
	σ	1.37	0.69	1.32	1.42	1.65	2.77	1.37	1.51
	R^2	.938	.997	.962	.986	.987	.839	.979	.955
LB$_{(0.2-0.8)}$	μ	6.29	5.34	4.22	5.00	4.79	5.06	5.57	5.18
	σ	0.82	0.32	2.72	1.59	0.61	0.30	0.98	1.05
	R^2	.989	.993	.918	.935	1.000	.996	.993	.975
NB$_{(0.5-0.5)}$	μ	5.57	6.11	4.99	5.10	5.75	4.95	6.58	5.58
	σ	0.99	1.24	1.29	0.21	1.40	1.10	2.02	1.18
	R^2	.997	.971	.981	.969	.976	.949	.897	.963
SB$_{(0.8-0.2)}$	μ	5.12	5.70	5.59	5.24	5.87	5.32	5.48	5.47
	σ	1.32	1.22	0.87	1.03	0.74	2.99	1.78	1.42
	R^2	.984	.991	.997	.989	.969	.863	.967	.966
SB$_{(0.9-0.1)}$	μ	5.63	5.21	6.31	4.31	7.32	6.53	8.19	6.21
	σ	1.36	0.01	1.27	0.96	2.25	2.33	1.77	1.42
	R^2	.992	1.000	.994	.998	.879	.990	.991	.978

Appendix E

Individual best-fitting parameters in Experiment 2, Chapter III: Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Table E1

Cumulative Gaussian Distribution

Condition	Parameter	PG39	PG18	P456	P960	P1727	P737	Average
	μ	5.09	4.51	5.88	7.69	5.52	6.38	5.85
$LB_{(0.2-0.8)}$	σ	1.24	1.54	1.00	1.06	2.34	1.43	1.44
	R^2	.995	.982	.944	.995	.993	.988	.983
	μ	5.51	5.72	6.22	9.60	7.09	7.30	6.91
$NB_{(0.5-0.5)}$	σ	0.84	1.59	0.5	2.24	1.87	1.97	1.50
	R^2	.983	.997	.996	.994	.997	.992	.993
	μ	6.91	5.51	7.05	8.41	7.08	7.82	7.13
$SB_{(0.8-0.2)}$	σ	1.41	0.84	2.15	0.63	0.9	1.15	1.18
	R^2	.977	.990	.985	.991	.993	.992	.988

Table E2

Empirical Cumulative Distribution Function of Departure Times

Condition	Parameter	PG39	PG18	P456	P960	P1727	P737	Average
	M	4.90	4.66	5.19	5.79	4.47	6.94	5.33
$LB_{(0.2-0.8)}$	*SD*	1.58	1.91	1.70	1.16	1.34	2.09	1.63
	R^2	.947	.927	.863	.623	.727	.957	.841
	M	5.59	5.31	5.76	5.38	5.16	5.80	5.50
$NB_{L(0.5-0.5)}$	*SD*	1.70	1.19	1.22	1.49	1.05	1.53	1.36
	R^2	.971	.963	.820	-.114	.583	.772	.666
	M	5.75	6.25	5.93	5.71	4.72	13.26	6.94
$SB_{(0.8-0.2)}$	*SD*	1.61	1.42	1.19	1.02	1.03	3.08	1.56
	R^2	.830	.986	.851	.362	.141	.867	.673

Appendix F

Number of "long" Choices/Location at Sample Offset for Each Intermediate Duration in Conditions LB and SB in Experiment 2, Chapter II (Pooled Across Birds)

Location	**NB**$_{(0.5-0.5)}$			**LB**$_{(0.2-0.8)}$			**SB**$_{(0.8-0.2)}$		
	4.2 s	**6 s**	**8.5 s**	**4.2 s**	**6 s**	**8.5 s**	**4.2 s**	**6 s**	**8.5 s**
1	0/61	9/40	0/0	2/63	10/35	6/8	3/69	9/33	3/8
2	0/29	6/25	5/7	0/6	4/17	0/3	0/22	4/28	2/6
3	0/10	17/33	5/15	2/21	15/23	4/5	0/15	7/26	5/11
4	0/0	6/8	15/24	2/3	6/7	10/12	0/2	8/17	13/17
5	1/1	1/2	7/7	0/0	4/5	19/19	0/0	1/1	19/22
6	5/7	0/0	54/55	11/15	19/21	60/61	0/0	1/3	43/44

Appendix G

Parameters obtained from individual cumulative Gaussian fits of psychometric functions in Experiment 1, Chapter IV: Lower asymptote (α), Upper asymptote (β), Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Condition	Parameter	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	Mean	*SEM*
LB	α	.04	.45	.07	.23	.01	.00	.00	.17	.29	.29	.32	.00	.16	.05
	β	.25	.07	.22	.00	.08	.04	.16	.11	.09	.00	.00	.02	.09	.02
	μ	0.55	0.55	0.57	0.58	0.56	0.52	0.56	0.56	0.54	0.62	0.53	0.52	0.56	0.01
	σ	0.02	0.02	0.06	0.04	0.03	0.08	0.06	0.04	0.03	0.07	0.02	0.04	0.04	0.01
	R^2	.97	1.00	.98	.96	.98	1.00	.99	.96	1.00	.67	1.00	.99	.96	.03
NB	α	.00	.14	.10	.05	.01	.01	.20	.16	.33	.00	.00	.07	.09	.03
	β	.14	.03	.00	.10	.03	.04	.38	.22	.05	.37	.01	.02	.12	.04
	μ	0.56	0.55	0.60	0.57	0.57	0.55	0.54	0.55	0.58	0.53	0.53	0.57	0.56	0.01
	σ	0.05	0.02	0.07	0.02	0.04	0.04	0.01	0.07	0.01	0.12	0.04	0.04	0.04	0.01
	R^2	.89	1.00	.98	1.00	.96	1.00	.98	1.00	.95	.79	.99	1.00	.96	.02
SB	α	.17	.00	.26	.00	.04	.07	.19	.00	.00	.03	.00	.03	.07	.03
	β	.00	.00	.32	.15	.19	.12	.19	.13	.08	.77	.06	.00	.17	.06
	μ	0.64	0.55	0.56	0.56	0.60	0.60	0.58	0.53	0.57	0.56	0.51	0.57	0.57	0.01
	σ	0.07	0.08	0.02	0.03	0.04	0.01	0.06	0.05	0.09	0.00	0.02	0.03	0.04	0.01
	R^2	.82	.84	1.00	.98	1.00	1.00	1.00	.94	.92	.85	.95	.99	.94	.02

Appendix H

Individual best-fitting parameters in Experiment 2, Chapter IV: Lower asymptote (α), Upper asymptote (β), Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Table H2

Cumulative Gaussian Distribution

Condition	Parameter	P1	P2	P3	P4	P5	P6	Mean	*SEM*
CRF	α	.24	.03	.08	.00	.00	.04	.07	.04
	β	.07	.00	.17	.03	.07	.21	.09	.03
	μ	1.68	1.99	1.89	1.64	1.21	1.63	1.67	0.11
	σ	0.08	0.54	0.15	0.24	0.16	0.07	0.21	0.07
	R^2	.96	.96	.98	1.00	1.00	.99	.98	.01
NB	α	.18	.00	.32	.00	.10	.25	.14	.05
	β	.18	.13	.26	.11	.15	.28	.19	.03
	μ	1.79	1.54	1.81	1.44	1.19	1.61	1.56	0.09
	σ	0.51	0.53	0.08	0.16	0.10	0.01	0.23	0.09
	R^2	.96	.99	.87	.99	.88	.95	.94	.02
LB	α	.08	.00	.02	.09	.02	.10	.05	.02
	β	.06	.06	.08	.04	.02	.06	.05	.01
	μ	1.55	1.47	1.90	1.73	1.32	1.97	1.66	0.10
	σ	0.19	0.70	0.32	0.08	0.07	0.30	0.28	0.09
	R^2	1.00	.84	1.00	1.00	1.00	.99	.97	.03
SB	α	.08	.00	.01	.00	.00	.04	.02	.01
	β	.35	.00	.06	.02	.04	.04	.09	.05
	μ	1.60	1.98	2.37	1.69	1.45	2.07	1.86	0.14
	σ	0.09	0.83	0.47	0.27	0.52	0.48	0.44	0.10
	R^2	.98	.84	1.00	1.00	.94	1.00	.96	.03

Table H3

Empirical Cumulative Distribution of Departure Times

Cond.	Parameters	P1	P2	P3	P4	P5	P6	Mean	*SEM*
CRF	*M*	1.53	1.60	1.72	0.73	1.51	1.91	1.50	0.18
	SD	0.53	0.32	0.42	0.12	0.28	0.41	0.35	0.06
	R^2	.82	.71	.85	.62	.90	.79	.78	.04
NB	*M*	2.08	1.65	1.34	2.00	1.49	1.85	1.73	0.13
	SD	0.49	0.34	0.73	1.13	0.36	0.68	0.62	0.13
	R^2	.93	.95	.86	.58	.73	.73	.80	.06
LB	*M*	1.79	1.60	1.71	2.54	1.61	1.63	1.81	0.16
	SD	0.36	0.28	0.28	0.39	0.33	0.69	0.39	0.06
	R^2	.97	.69	.88	.63	.92	.98	.84	.06
SB	*M*	2.07	1.47	1.87	2.36	1.58	2.10	1.91	0.15
	SD	0.42	0.23	0.27	0.36	0.36	0.46	0.35	0.04
	R^2	.80	.81	.78	.73	.83	.99	.83	.04

Appendix I

Sound clips used in the temporal bisection task from Experiment 2

Task Sound	Title	Description	Download Link	Uploaded by Date (mm.dd.yy)
Sample	Computer Sci Fi	Science fiction machine processing data	http://soundbible.com/561-Computer-Sci-Fi.html	BlastwaveFx* (06.13.09)
Shots fired	Laser	Laser shooting sound	http://soundbible.com/1087-Laser.html	Mike Koenig* (10.10.09)
Correct feedback	Shotgun Blast	Single shotgun blast or explosion	http://soundbible.com/1919-Shotgun-Blast.html	Jim Rogers* (08.19.11)
Incorrect/Non-baited feedback	Flyby	A whooshing sound	http://soundbible.com/1891-Flyby.html	Conor* (07.18.11)
Level up	Power Up	A powering up noise like a spaceship	http://soundbible.com/1639-Power-Up.html	Public Domain (12.01.10)
End of session	Sports Crowd	A crowd at a sports center or sporting event	http://soundbible.com/1881-Sports-Crowd.html	GoGo* (07.11.11)

Note. * Credit for files licensed under Creative Commons Attribution 3.0.

Appendix J

Parameters obtained from individual cumulative Gaussian fits of psychometric functions in Experiment 1, Chapter V: Lower asymptote (α), Upper asymptote (β), Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Condition	Parmameter	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	Mean	*SEM*
LB	α	.00	.00	.00	.00	.18	.00	.00	.18	.12	.00	.25	.00	.07	.03
	β	.07	.03	.10	.23	.00	.16	.12	.05	.17	.00	.05	.14	.09	.02
	μ	0.56	0.55	0.52	0.55	0.65	0.54	0.56	0.56	0.59	0.57	0.56	0.58	0.57	0.10
	σ	0.03	0.04	0.06	0.07	0.01	0.03	0.04	0.03	0.05	0.04	0.03	0.05	0.04	0.00
	R^2	1.00	.99	1.00	.88	.95	.98	1.00	.96	.93	.99	.97	.96	.97	.01
NB	α	.05	.20	.09	.27	.08	.15	.15	.34	.00	.08	.00	.07	.12	.03
	β	.03	.10	.08	.42	.43	.17	.28	.10	.28	.00	.02	.13	.17	.04
	μ	0.60	0.58	0.57	0.55	0.60	0.56	0.59	0.62	0.57	0.57	0.53	0.57	0.58	0.07
	σ	0.02	0.02	0.04	0.01	0.00	0.00	0.02	0.01	0.06	0.03	0.05	0.02	0.02	0.01
	R^2	.98	1.00	1.00	.84	.92	.98	.99	.98	.74	1.00	1.00	.95	.95	.02
SB	α	.00	.09	.02	.07	.14	.31	.11	.11	.00	.09	.00	.00	.08	.03
	β	.00	.21	.15	.00	.00	.09	.03	.00	.20	.14	.23	.20	.10	.03
	μ	0.58	0.62	0.54	0.59	0.65	0.55	0.55	0.58	0.56	0.55	0.52	0.54	0.57	0.01
	σ	0.01	0.06	0.04	0.04	0.03	0.01	0.03	0.08	0.06	0.02	0.04	0.04	0.04	0.01
	R^2	1.00	.95	.97	.96	.98	.98	1.00	.98	.90	.96	.91	.99	.97	.01

Appendix K

Individual best-fitting parameters in Experiment 2, Chapter IV: Lower asymptote (α), Upper asymptote (β), Mean (μ), Standard Deviation (σ), and Coefficient of Determination (R^2)

Table K2

Cumulative Gaussian Distribution

Condition	Parameter	P1	P2	P3	P4	P5	P6	Mean	*SEM*
CRF	α	.00	.00	.00	.00	.08	.00	.01	.01
	β	.13	.00	.00	.01	.04	.00	.03	.02
	μ	1.98	1.95	1.60	1.61	1.75	1.62	1.75	0.07
	σ	0.31	0.26	0.13	0.33	0.27	0.10	0.23	0.04
	R^2	.97	1.00	1.00	1.00	.99	1.00	.99	.00
NB	α	.04	.00	.02	.00	.00	.02	.01	.01
	β	.02	.00	.00	.00	.05	.03	.02	.01
	μ	2.40	2.01	1.42	1.57	1.43	1.53	1.73	0.16
	σ	0.27	0.41	0.13	0.15	0.32	0.15	0.24	0.05
	R^2	1.00	1.00	1.00	1.00	.99	.99	1.00	.00
LB	α	.00	.00	.00	.00	.00	.00	.00	.00
	β	.00	.00	.03	.00	.03	.00	.01	.01
	μ	1.75	1.85	1.60	1.66	1.61	1.57	1.67	0.04
	σ	0.11	0.26	0.12	0.14	0.50	0.16	0.21	0.06
	R^2	1.00	1.00	.99	1.00	.95	1.00	.99	.01
SB	α	.00	.00	.00	.00	.00	.00	.00	.00
	β	.00	.00	.00	.03	.03	.00	.01	.01
	μ	1.72	1.57	1.90	1.49	1.48	1.54	1.62	0.07
	σ	0.12	0.12	0.22	0.14	0.26	0.15	0.17	0.02
	R^2	1.00	1.00	1.00	.99	.99	1.00	1.00	.00

Table K3

Empirical Cumulative Distribution of Departure Times

Cond.	Parameters	P1	P2	P3	P4	P5	P6	Mean	*SEM*
CRF	*M*	1.53	1.60	1.72	0.73	1.51	1.91	1.50	0.18
	SD	0.53	0.32	0.42	0.12	0.28	0.41	0.35	0.06
	R^2	.82	.71	.85	.62	.90	.79	.78	.04
NB	*M*	2.08	1.65	1.34	2.00	1.49	1.85	1.73	0.13
	SD	0.49	0.34	0.73	1.13	0.36	0.68	0.62	0.13
	R^2	.93	.95	.86	.58	.73	.73	.80	.06
LB	*M*	1.89	1.78	2.03	2.08	1.8	1.96	1.92	0.05
	SD	0.13	0.15	0.31	0.39	0.5	0.27	0.29	0.06
	R^2	1.00	.87	.86	.82	.96	.99	.84	.06
SB	*M*	1.96	2.03	2.2	2.1	2.09	2.01	2.07	0.03
	SD	0.14	0.42	0.47	0.22	0.68	0.29	0.37	0.08
	R^2	1.00	.87	.86	.82	.83	.99	.83	.04