Adaptive Modulation of Time-Based Decisions by Probabilistic Contingencies

by

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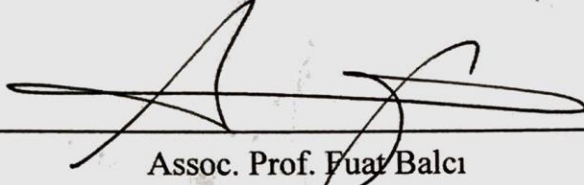at the Koç University

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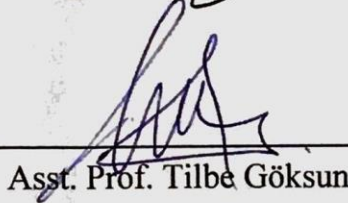
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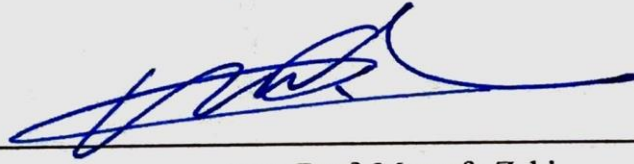
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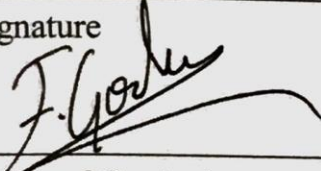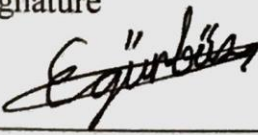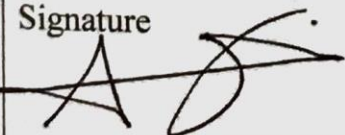
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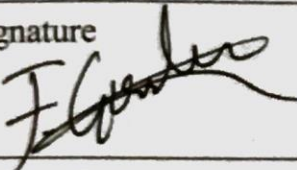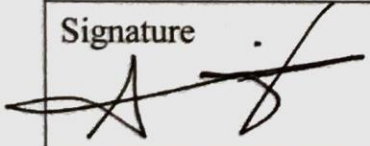
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Abstract

This thesis investigated the effect of experienced probabilistic contingencies on the temporal decisions of humans and mice and evaluated the observed alterations in decision outputs within the framework of optimality. The first study aimed to evaluate the optimality of two-alternative forced (retrospective temporal) choice behavior of human participants under different stimulus probabilities and payoff matrices (with or without penalty for erroneous decisions). The results of this study showed that human participants adapted their two-alternative time-based decisions in response to the manipulations of stimulus probabilities and nearly maximized their gain irrespective of the payoff matrix. The second study aimed to investigate the generalizability of optimal temporal decision-making performance of humans and mice to conditions with more than two temporal options. In this experiment, the probabilities of different options were manipulated between experimental conditions and subjects were required to make two sequential temporal decisions within a trial (as opposed to a single decision in the first study). The results of this study revealed that the number of temporal options constituted a limiting factor for the optimality of human time-based decision making. Although, humans could adapt their initial decisions in response to probabilistic information, their subsequent decisions were not sensitive to probabilistic relations. On the other hand, mice could adapt both their initial and subsequent decisions in response to probabilistic contingencies. These experiments extended the scope of temporal risk-assessment studies to include retrospective decision-making and defined a limiting factor for human optimal time-based decisions.

Keywords: Time discrimination, Optimality, Reward maximization

Özet

Bu tezde deneyim edilmiş olasılıksal ilişkilerin insanların ve farelerin zamansal kararları üzerindeki etkisi incelendi ve karar çıktılarında gözlenen değişiklikler optimallik çerçevesinde değerlendirildi. İlk çalışmada, insanların farklı uyaran olasılıkları ve sonuç matrisleri (hatalı kararlar için ceza ile veya ceza olmadan) ile ilişkili iki alternatifli zorunlu (geriye dönük zamansal) seçim davranışının optimalliğinin değerlendirilmesi amaçlanmıştır. Bu çalışmanın sonuçları, uyaran olasılıklarının manipülasyonlarına karşılık olarak katılımcıların iki alternatifli zamana bağlı kararlarını adapte ettiklerini ve test edilen iki sonuç matrisinde de elde edilen kazancın maksimizasyonuna çok yaklaştıklarını göstermiştir. İkinci çalışmada, optimal zamansal karar verme performansının ikiden fazla zamansal seçeneğin bulunduğu durumlara genelleştirilebilirliğinin, hem insan hem de farelerde araştırılması amaçlanmıştır. Bu deneyde, farklı seçeneklerin olasılıkları deneysel koşullar arasında manipüle edilmiş ve katılımcıların bir deneme içinde iki sıralı zamansal karar (ilk çalışmadaki tek bir karardan farklı olarak) vermeleri beklenmiştir. Bu çalışmanın sonuçları, zamansal seçenek sayısının insanlarda zamana bağlı kararların optimalliği için kısıtlayıcı bir unsur teşkil ettiğini ortaya koymuştur. Her ne kadar insanlar olasılıksal bilgilere karşılık ilk kararlarını adapte edebilseler de, daha sonraki kararlarının olasılıksal ilişkilere duyarlı olmadığı gözlenmiştir. Öte yandan, fareler olasılıksal ilişkilerin manipülasyonuna karşılık hem ilk hem de sonraki kararlarını adaptif bir biçimde değiştirebilmişlerdir. Bu deneyler, zamansal risk değerlendirme çalışmalarının kapsamını, geriye dönük kararları içerecek şekilde genişletmiş ve insanların zamana bağlı kararlarının optimalliği için sınırlayıcı bir koşulu tanımlamıştır.

Anahtar Sözcükler: Zaman ayrıştırma, Optimalite, Ödül maksimizasyonu

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Introduction

Animals and humans make many simple but critical decisions based on time intervals. Whether a simple decision such as catching a bus or a critical decision such as taking pills on time, many time-based decisions require statistical analysis of temporal information. A number of previous studies have shown that decision-makers' endogenous timing uncertainty accompanied by probabilistic contingencies and payoff information are important for the optimization of temporal decisions (Balcı et al., 2011; Brunner, Kacelnik, & Gibbon, 1992; Çavdaroğlu, Zeki, & Balcı, 2014; Kacelnik, Brunner, & Gibbon, 1990; Kheifets & Gallistel, 2012). Studies of temporal decision making showed nearly optimal performance of humans and mice on temporal discrimination procedures (Balcı, Freestone, & Gallistel, 2009; Kheifets & Gallistel, 2012). However the generalizability of these findings are limited since the procedures mostly relied on prospective decision making and featured two reference temporal options. The main purpose of the current studies was to investigate the effect of probabilistic manipulations on temporal discrimination performance of humans and mice within the optimality framework. The first study aimed to expand the scope of earlier work by evaluating the effect of different probabilistic contingencies and different payoff matrices on temporal decision outputs of humans in a retrospective decision making task (temporal bisection task). The second study aimed to investigate the limiting conditions for the optimal temporal decision-making by investigating the effect of exogenous probabilistic contingencies on temporal decisions of humans and mice between multiple (i.e., three) temporal options.

Humans and non-human animals are able to perceive time intervals from seconds to minutes presumably with a stopwatch-like mechanism as a result of their evolutionary history (Buhusi & Meck, 2005). For instance, animals organize their activities over biologically

important time intervals (Drew, Zupan, Cooke, Couvillion, & Balsam, 2005), compute reward rates that require the estimates of time intervals (Gallistel et al., 2007), and make other critical temporal decisions (Kacelnik & Brunner, 2002). The statistical properties of interval timing demonstrated that humans and other animals exhibit high accuracy but limited precision in their close to normally-distributed timed responses. Importantly, the trial-to-trial variability in temporal responses exhibits the scalar property; the standard deviation of time estimates is proportional to their means (i.e., constant coefficient of variation; Buhusi & Meck, 2005; Gibbon, 1977; Gibbon, Church, & Meck, 1984; Simen, Rivest, Ludvig, Balci, & Killeen, 2013). Thereby, the statistical properties of timing behavior are very important to understand the dynamics that underlay temporal decision-making and their optimality.

Kahneman and Tversky (1979) argued that humans are irrational decision makers about probabilistic prospects. One can test this claim also in the domain of temporal decision-making by taking into account the psychophysics of interval timing. As stated above, there is now a rich set of previous studies that showed that the decision maker's level of endogenous timing uncertainty (coefficient of variation) is one of the primary variables that determine the optimal temporal decision strategies (Balcı et al., 2009; Balcı et al., 2011; Jazayeri & Shadlen, 2010; Kheifets & Gallistel, 2012; Simen, Balcı, Cohen, & Homes, 2011).

The number of studies that investigate reward maximizing decision-making strategies in temporal discrimination procedures is increasing. One of the temporal discrimination procedures that has been used in these studies is the switch task (Balcı et al., 2008; Killeen & Fetterman, 1988; Platt & Davis, 1983). In a given trial of this task, subjects decide to stay in a location that delivers reward after a short delay or leave this location (if reward is not delivered there after the short delay) for another location that delivers reward after a long delay. This behavioral pattern emerges because the trial type (i.e., the active location in a trial) is not signaled by a discriminative stimulus in a given trial. If the participants are at the

incorrect location at the active reward delivery time, they either miss the reward or experience penalty (depending on the payoff matrix). In this sense, switching earlier than the short trial duration and failing to switch before the long trials can lead to opportunity cost or penalty depending on the active trial type.

Balcı et al. (2009) used the switch task by manipulating the relative frequencies of short and long trials and evaluated the performance of humans and mice within the optimality framework. The results showed that subjects adjusted their temporal decisions to the probabilistic manipulations of different trial types; the switch latencies were shorter when the short trial probability was low and longer when the short trial probability was high. In addition, these researchers found that by adapting temporal decisions subjects could maximize the expected gains in this task. In a more recent study, Kheifets and Gallistel (2012) pointed at similar results by using the same task in mice. Different from Balcı et al. (2009), their study showed that mice can rapidly and abruptly adapt their temporal decisions in an optimal fashion in response to changing probabilities of different trial types. Overall, these findings suggest that human and non-human animals could nearly optimize their time-based decisions in the temporal switch task.

One of the limitations of these earlier studies is that they used prospective decision-making tasks. In other words, subjects made their time-based decisions during the timing stimulus. However, temporal decisions about events that have already happened (retrospective) might also provide valuable information in the context of reward maximization (e.g., response times). The temporal bisection task enables studying temporal decisions that are made retrospectively. In this task, subjects are asked to categorize time intervals (short, intermediate, long) as short or long after the cessation of stimulus duration in order to earn reward. No feedback is provided for the categorizations of the intermediate durations in order to capture the perceptual aspects of timing. Importantly, the temporal

bisection task would be the retrospective analogue of the switch task. In the first experiment, we used the temporal bisection task to investigate the effects of stimulus probabilities on the retrospective temporal decision-making in humans.

Another limitation of the earlier studies is that the temporal discrimination procedures used with humans and animals contained only two probabilistic options. On the other hand, in real-life decisions scenarios humans and animals are confronted with multiple and/or sequential temporal decisions. For instance, assume that you are a driver for the school bus and sometimes your passengers do not show up on time. How much time do you allocate for each passenger without running late to the destination? The question of whether and how humans and non-humans adapt their temporal decisions in response to multiple probabilistic relations was not studied before.

On the other hand, the differences between single and multiple decision making strategies were indicated in the domain of optimal temporal motor planning. Many studies showed that humans could optimize their decision-making performance on a single isolated timed movement tasks (Battaglia & Schrater, 2007; Dean, Wu, & Maloney, 2007; Hudson, Maloney, & Landy, 2008). In one study, participants were required to touch a computer screen within a specific time window to get a reward (Hudson et al., 2008). Touching the screen at another time window resulted in penalty. Hudson et al. (2008) found that human participants adjusted their motor endpoints optimally on this single movement task. On the other hand, a sequential visio-motor study conducted by Wu, Dal Martello, and Maloney (2009) demonstrated that humans were suboptimal in allocating time to different options. In this study, participants were required to touch a computer screen with two targets in order to earn reward. The amount of reward for each target varied across conditions. If subjects failed to complete both movements within a 400 ms time limit, they received no reward at all. Wu et al. (2009) found a suboptimal tendency in this sequential movement planning task such

that participants spent more time on the first target even though the related payoff for the second target was much larger. Therefore, overall results suggest the numbers of targets might be a limiting factor for the optimal temporal decision-making.

The literature that uses the modulatory effects of probabilistic information on temporal discrimination tasks is increasing (Balcı et al., 2009; Kheifets & Gallistel, 2012). Research with further critical experimental manipulations can help elucidate the nature and/or the boundaries of optimal temporal behavior. Thus, in Study 1, the effect of stimulus probability on retrospective temporal judgments was investigated within the optimality framework. In Study 2, the optimality of timed decisions that encompass multiple options was studied using the temporal switch task. Testing both humans and mice has added translational power to the second study by enabling the comparison of the results across species. The two studies conducted broadened the scope of existing literature on optimal temporal behavior.

Study 1

1. Methods

a. Subjects. A total of 48 university students served as participants in this study: 24 participants (17 females, 7 males; age, M=23.25 years, SD=3.8) were tested in Group 1, and 24 participants (18 females, 6 males; age M= 20.83 years, SD=2.48) were tested in Group 2. The participants were recruited through a publically available newsletter on the Koç University website. The experiment comprised two 50-minute-long (fixed session duration) daily temporal bisection sessions and one 10-minute-long visual discrimination task after the second temporal bisection session. The participants received monetary rewards based on their performance in all three experimental sessions.

b. Stimuli and apparatus. In the *temporal bisection task*, the timing stimuli included a square (40 × 40 pixels) presented in the middle of the screen with a black background. The period for which the square was visible on the screen was the timing signal. All sessions had fixed durations and the participants could take a break in between the test blocks. The display was generated in MATLAB on a Macintosh computer, using the Psychophysics Toolbox extension (Kleiner, Brainard, & Pelli, 2007). The responses were collected with a computer keyboard.

c. Procedure.

The temporal bisection task.

Familiarization. The participants were presented with the two reference durations (1000 ms vs 1500 ms) four times in an alternating order, followed by text indicating whether it was a short or long reference.

Practice. Short and long durations were presented in a pseudo-random order. Participants categorized these durations as short or long by pressing the "V" key with their left and the "N" key with their right index finger, respectively. The practice phase continued for at least 30 trials and until the discrimination accuracy in the last 25 trials was at least 90%. The participants received feedback about the accuracy of their categorizations. For correct categorizations, a brief beep sound was played and the text "Correct" was presented in green for 750 ms at the top of the screen. For errors, a brief buzzer sound was played, and the text "Incorrect" was presented in red for 750 ms at the top of the screen. The participants were asked not to respond prior to the cessation of the stimulus that signaled the time interval to be judged. In case of key presses during the stimulus (premature) or wrong key presses (keys other than "V" or "N"), a warning phrase was presented in purple for 1250 ms. For

each condition, probabilities of short and long reference durations were manipulated (see below). The participants did not accrue any points during the practice phase.

Test. Five different conditions were defined based on different reference duration probabilities ($p(T_{\text{Short}})/[p(T_{\text{Short}}) + p(T_{\text{Long}})]$) =.10, .25, .50, .75, or .90, referred to as $p(T_S)$). Note that sum of $p(T_{\text{Short}}) + p(T_{\text{Long}})$ was always .36 (see below for details). Each participant was tested on one of the four unequal probability conditions in one session and the equal probability condition in the other (order counterbalanced). The participants were informed that, unlike the practice phase, in the test phase intermediate durations would be presented intermixed with the reference durations and that they should categorize each duration as short or long (Figure 1). Each set contained nine durations (including the reference durations), spaced at logarithmically equal distances. Intermediate durations were 1052, 1107, 1164, 1225, 1288, 1355, and 1426 ms and constituted 64% of the trials, with an average of 424 intermediate duration trials per participant for each session (Group 1 and 2). The participants were only rewarded for their correct categorizations of the reference durations in both groups. In Group 1 the participants were not penalized for incorrect categorizations of the reference durations (only feedback was provided) whereas in Group 2 the participants were penalized for incorrect categorizations ($-2 \times$ Reward). Neither feedback nor reward was provided for the categorization of the intermediate durations in order to capture the purely perceptual aspects of temporal discrimination (note that there is no absolute correct categorization for an intermediate duration). The participants were asked to respond as accurately and quickly as possible. This instruction was provided particularly because the response times constituted a unit of analysis in this study. Since the participants could not respond during the timing stimulus, the response time (RT) measurements started at the end of the stimulus that signaled the to-be-judged duration. The participants could take a break and restart testing after every tenth trial (except during the first 30 practice trials).

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Two-back working memory secondary task. The participants were instructed not to count or engage in any rhythmic activity such as tapping. In order to prevent chronometric counting, the participants were tested on a concurrent two-back working memory task. After each categorization response, a number selected randomly from 1 to 9 was presented in the middle of the screen for 750 ms. The participants were told that after some trials they would be asked to recognize the number they had seen two trials ago. The number of trials between working memory "interrogations" was sampled from a truncated Poisson distribution (lower bound of 3 and upper bound of 30) with a mean of 10. In the interrogation trials, a number, with *p*(*target*) =.50, was presented and the participants were asked to press "V" if it was the number they saw two trials back and "N" if not. The participants received feedback regarding the accuracy of their working memory performance (for 1000 ms).
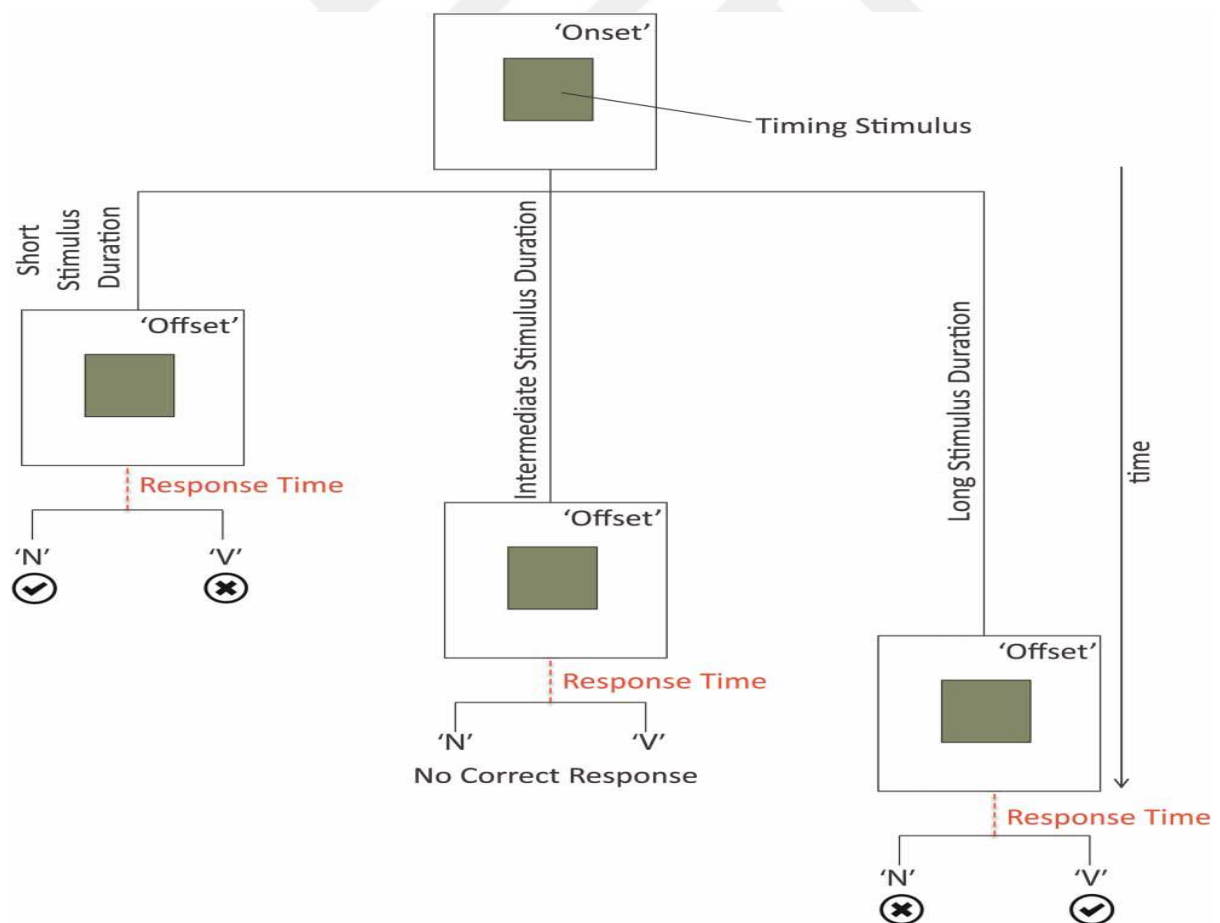
Figure 1. Graphical depiction of the temporal bisection task.

The inter-trial intervals were sampled from a truncated exponential with a mean of 500 ms and an upper bound of 1 s. At the beginning of the experiment, the participants were told that their earnings from the timing trials would be weighted by the proportion of correct responses in the working memory task. They were informed about their cumulative earnings during each break. A participant could earn on average up to TRY15 (~USD8) in a single temporal bisection session.

Visual discrimination task. The temporal bisection task was ran as it is typically reported in the literature, namely the use of the left hand for short and the right hand for long categorizations. However, in order to control for possible biases in the left- and right-hand response times, the participants were tested on a visual discrimination task in the last session. This task required them to respond using either their left ("V" key) or right index finger ("N" key) contingent upon the location of a black circle presented either on the right or the left side of the square in a pseudo-randomized order (TRY.01 per correct response). The participants were instructed to be as fast and accurate as possible. A brief beep sound was played for correct answers and a brief buzzer sound for errors. The participants could take a break and restart testing by pressing a key after every twentieth trial.

d. Data analysis. Points of subjective equality, coefficients of variation, and response times were compared between unequal probability conditions using the Kruskal-Wallis test and, where appropriate, follow-up pair-wise comparisons were conducted using the Mann-Whitney test. Data collected from paired equal and unequal probability conditions were compared with Wilcoxon signed rank tests. One-way ANOVA and t-test comparisons revealed the same results in all but one of the comparisons conducted (i.e., comparison of PSEs between four different equal probability groups—used as controls for unequal probability conditions for each subject). An alpha level of .05 (two-tailed) was used for all statistical analyses. Any RT that was longer than 2 s (0.63% of trials in Group 1 and 0.29%

trials in Group 2) was excluded from the RT analyses. Three participants in Group 2 did not attend the visual discrimination task.

   Optimality analysis. The expected gain in the temporal bisection task can be calculated as in the switch task (Balcı et al., 2009). Although in the switch task the participants physically switch from the location associated with short duration to the other location associated with long duration, in the case of temporal bisection task they can be considered as switching from a short categorization state to a long categorization state as time elapses (e.g., Machado & Keen, 2003). The reward maximization here requires participants to take account of not only exogenous probabilities, i.e., $p(T_S)$, but also their own timing uncertainty, i.e., CV. This relation is described in detail below.

   The choice proportions gathered from the temporal bisection task can be well described as a cumulative Gaussian distribution (fit using least squares method in our study); the mean of the best-fit normal cumulative distribution function can be treated as the targeted point of subjective equality (PSE; criterion) and its CV can be treated as an index of timing uncertainty. The expected gain for a given estimate of timing uncertainty (CV), reference duration probabilities, and payoff matrix (payoffs associated with two correct and two incorrect categorizations) can be computed for different possible target PSEs. The target bisection point that maximizes the expected gain can be identified as the optimal target PSE for that given level of timing uncertainty and the corresponding task conditions (i.e., reference duration probabilities and payoff matrix). Here, the expected gain for a given target bisection point is the sum of the relative values of different consequences, where the relative value is the gain associated with a given consequence weighted by the probability of attaining it (Balcı et al., 2009). Specifically, it is the payoff matrix weighted by the probability of different consequences (correctly categorizing the short reference duration as short and long reference duration as long, and incorrectly categorizing the short reference duration as long

and long reference duration as short) determined jointly by the level of the participants'

endogenous timing uncertainty and the probability of short and long reference durations

(exogenous probabilities).

Equation 1 defines the expected gain for an estimate of the target bisection point ($\hat{t}$)

and the level of endogenous timing uncertainty ($\hat{w}$).

$$EG(\hat{t}) = g(\sim T_S)p(T_S)\Phi(T_S, \hat{t}, \varpi\hat{t})$$

$$+g(T_s)p(T_S)\big(1 - \Phi(T_S, \hat{t}, \varpi\hat{t})\big)$$

$$+ g(T_L)\big(1 - p(T_S)\big)\Phi(T_L, \hat{t}, \varpi\hat{t})$$

$$+ g(\sim T_L)\big(1 - p(T_S)\big)\big(1 - \Phi(T_L, \hat{t}, \varpi\hat{t})\big)$$

(1)

where $\hat{w} = \hat{\sigma}/\hat{t}$, $\hat{\sigma}$ is the standard deviation and $\hat{t}$ is the participant's target PSE, both of

which are estimated from fits to the participant's choice proportions (best-fitting standard

deviation and mean values). T_S and T_L are the short and long reference durations, $p(T_S)$ is the

probability of the short reference duration, g denotes the payoff matrix (e.g., $g(T_L)$ is the gain

associated with a correct categorization of the long reference duration, $g(\sim T_S)$ is the loss

associated with categorizing the short duration as long). $\Phi = 0.5\,[1 + erf\,((\mathrm{x} -$

$\hat{t}\,)/(\sqrt{2}\hat{w}\hat{t}))]$ is the normal cumulative distribution function with mean $\hat{t}$ and standard

deviation $\hat{w}\hat{t}$ that can be evaluated at any arbitrary time point in the trial such as the short

(T_S) or long (T_L) reference durations. These values can be computed for different possible $\hat{t}$s

and the optimal bisection point can be identified numerically by finding the $\hat{t}$ value that

maximizes the expected gain. For instance, Figure 5 shows expected reward curves calculated

according to Equation 1 for five different probability conditions and given levels of timing

uncertainty. The locations of the peaks of these curves are the optimal target bisection points

for the corresponding condition and the level of timing uncertainty. Note that, in order to

capture the scalar property (Gibbon, 1977) during these computations, $\hat{\sigma}$ is set proportional to

$\hat{t}$ based on the estimate of the participant's coefficient of variation.

Figure 2 depicts the relationship between the optimal temporal strategy and the level

of timing uncertainty for different exogenous probability conditions on the basis of the

expected gain function described above. Specifically, Figure 2 (left column; Group 1 & right-

hand; Group 2) shows the expected gains for different combinations of target PSEs and levels

of timing uncertainty (forming a heat map) after normalizing them by the maximum possible

expected gain for the corresponding level of timing uncertainty. The ridge of this normalized

surface indicated by the black curve constitutes the optimal performance curve that denotes

the optimal target PSEs for different levels of timing uncertainty separately for the five

different probability conditions demonstrating the dependence of optimal strategies on the

level of timing uncertainty in all of these conditions. Note that the optimal performance

curves are identical for Group 1 and Group 2 for the same exogenous probability conditions

due to the symmetrical payoff matrices. However, a given level of deviation from optimality

in terms of time units results in a larger loss in Group 2 due to the non-zero penalty for errors.

Note the curved shape of the optimal performance curve even when $p(T_S) = .50$. This is

essentially due to the relationship between mean and standard deviation assumed by the

scalar property of interval timing.
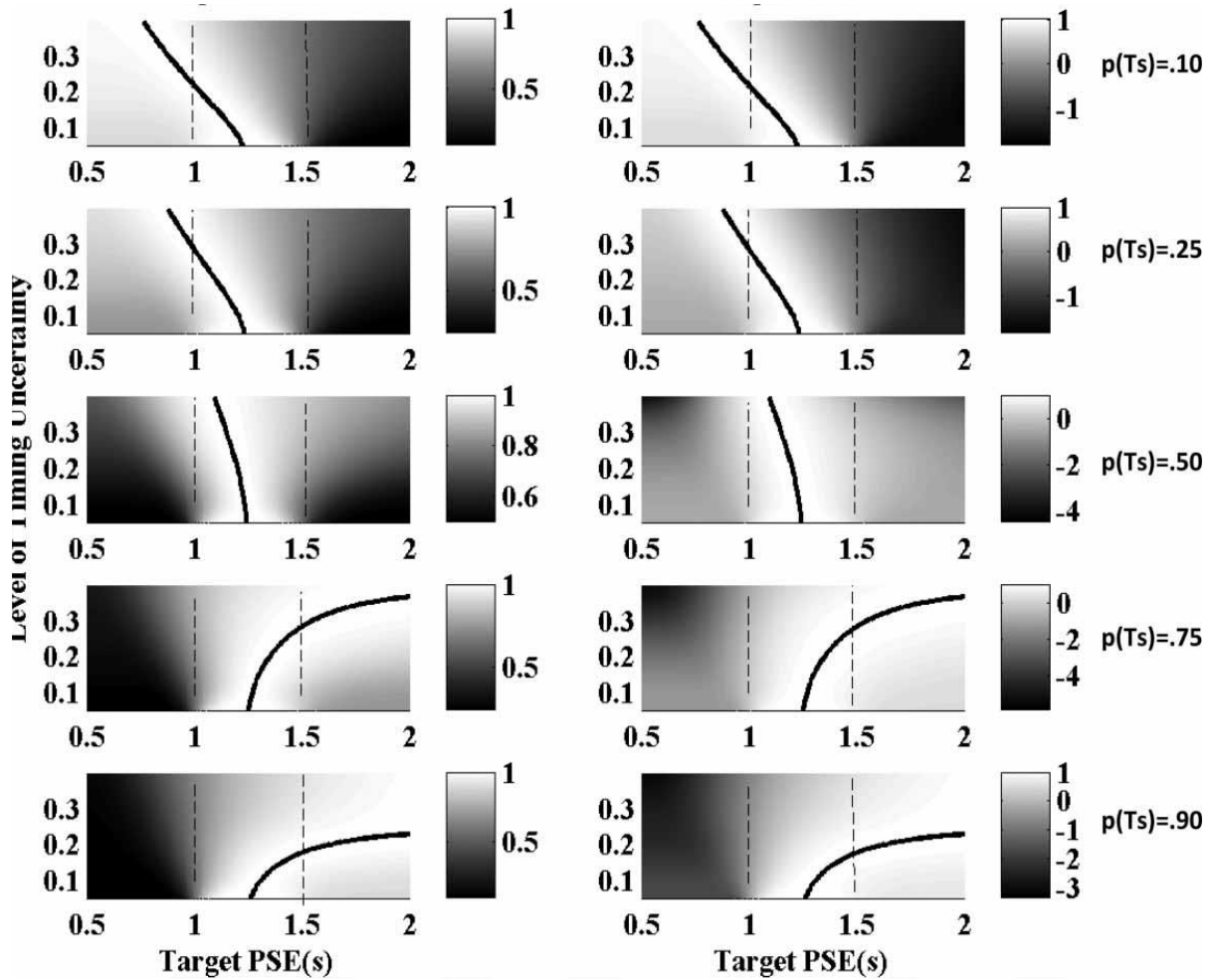
Figure 2. Normalized expected gain surfaces from perpendicular view as a function of target PSE ($\hat{t}$) and the level of timing uncertainty ($\hat{w}$) for five different probability conditions for the payoff matrix used in Group 1 (left column) and Group 2 (right column). Expected gains for each level of timing uncertainty ($\hat{w}$) have been normalized by the maximum possible expected gain that could be attained with that level of timing uncertainty. This defines a ridge (indicated by the black curves) over this surface with the same level of elevation, which defines the optimal performance curve for the corresponding task conditions. Optimal performance curves defined separately for different exogenous probability conditions prescribe the reward-maximizing target PSEs for different levels of timing uncertainty under the corresponding probability condition. Shades of grey indicate the proportion of normalized maximum expected gain. Note the dependence of optimal target PSEs on reference duration probabilities (different panels) as well as on the level of timing uncertainty (y-axis). The optimal performance curves are identical for Group 1 and Group 2 for the same exogenous probability conditions.

2. Results

e. Choice proportions. Figure 3, left and right panels, shows the choice proportions separately for five different probability conditions, along with the best-fit cumulative

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Gaussian distribution functions for Group 1 and Group 2, respectively. All R^2 values for these fits were over .97 in both Group 1 and Group 2. The median R^2 value for fits to individual participants' data was .97 for both groups. Figure 3 shows that participants modulated their choice behavior in the expected direction in response to the different experienced reference probabilities. Specifically, the psychometric function shifted leftward with decreasing and rightward with increasing short reference probabilities in both Group 1 and Group 2.
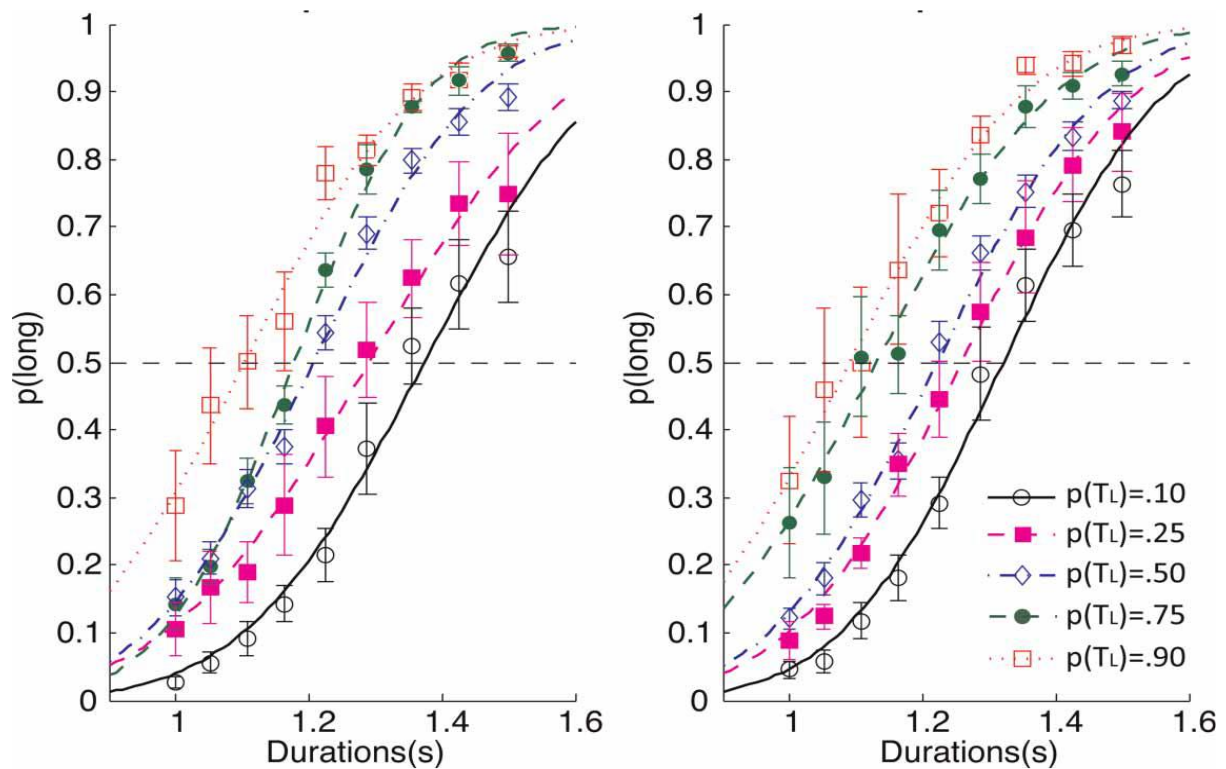
Figure 3. Choice proportions as a function of stimulus durations separately for five different short reference duration probabilities for Group 1 (left panel) and 2 (right panel). Curves are best-fit cumulative Gaussian distribution functions to the average choice proportions. Error bars stand for SEM.

The target PSE and the level of endogenous timing uncertainty (i.e., CV) were estimated from cumulative Gaussian fits to individual participants' choice proportions. Figure 4(A) and (B) shows that average empirical PSEs estimated from fits to the individual participants' data increased with increasing short reference duration probability, $F(1,3) = 64.53$, $p < .01$, $R^2 = .96$ (Group 1) and $F(1,3) = 178.40$, $p < .001$, $R^2 = .98$ (Group 2).

Empirical PSEs differed between equal and unequal probability conditions (within-group comparison) for all four pairs (all ps < 0.05) except for $p(T_S) = .25$ ($p = 0.14$) in Group 1 and except for $p(T_S) = .75$ ($p = 0.60$) in Group 2. When Holm-Bonferroni correction was applied, there were no significant differences. The between-group comparison of empirical PSEs between four unequal probability conditions revealed a significant overall difference, χ^2 (3, $N = 24$) $= 16.20$, $p < .01$, ($\eta^2 = .64$) in Group 1 and χ^2 (3, $N = 24$) $= 16.89$, $p < .001$ ($\eta^2 = .57$) in Group 2. The pair-wise comparisons revealed significant differences between the following pairs in Group 1: $p(T_S) = .10$ vs. $p(T_S) = .75$; $p(T_S) = .10$ vs. $p(T_S) = .90$; and $p(T_S) = .25$ vs. $p(T_S) = .90$ (all ps < 0.05, Holm-Bonferroni corrected). The pair-wise comparisons of unequal probability conditions revealed significant differences between the following pairs in Group 2: $p(T_S) = .10$ vs. $p(T_S) = .90$; $p(T_S) = .25$ vs. $p(T_S) = .75$; and $p(T_S) = .25$ vs. $p(T_S) = .90$ (all ps < 0.05, Holm-Bonferroni corrected). There were no significant differences between the four corresponding equal probability conditions in Group 1 (χ^2 (3, $N = 24$) $= 3.18$, $p = 0.37$) or Group 2 (χ^2 (3, $N = 24$) $= 6.56$, $p = 0.09$ (between-group comparison). Figure 4(C) and (D) shows the average empirical PSEs estimated from fits to the individual participants' data as a function of the average optimal PSEs calculated for each participant for his or her level of timing uncertainty separately for different reference probability conditions in Group 1 and Group 2, respectively. The thin lines show the orthogonal regression fits to these data. There was a significant relationship between the empirical and optimal PSEs for both Group 1, slope $= .66$, $p < .05$, and Group 2, slope $= .74$, $p < .01$. In Group 1, empirical PSEs were not significantly different from the optimal PSEs (within-group comparison) in any probability condition (all ps $\geq .24$) except for when $p(T_S) = .10$ ($p < .05$). In this condition, the empirical PSEs were significantly longer than the optimal PSEs ($p < .05$). In Group 2, empirical PSEs were not significantly different from the optimal PSEs (within-group comparison) in any

probability condition (all $ps \geq .24$) except for when $p(T_S) = .90$ ($p < .05$). In this condition, the

empirical PSEs were significantly shorter than the optimal PSEs.
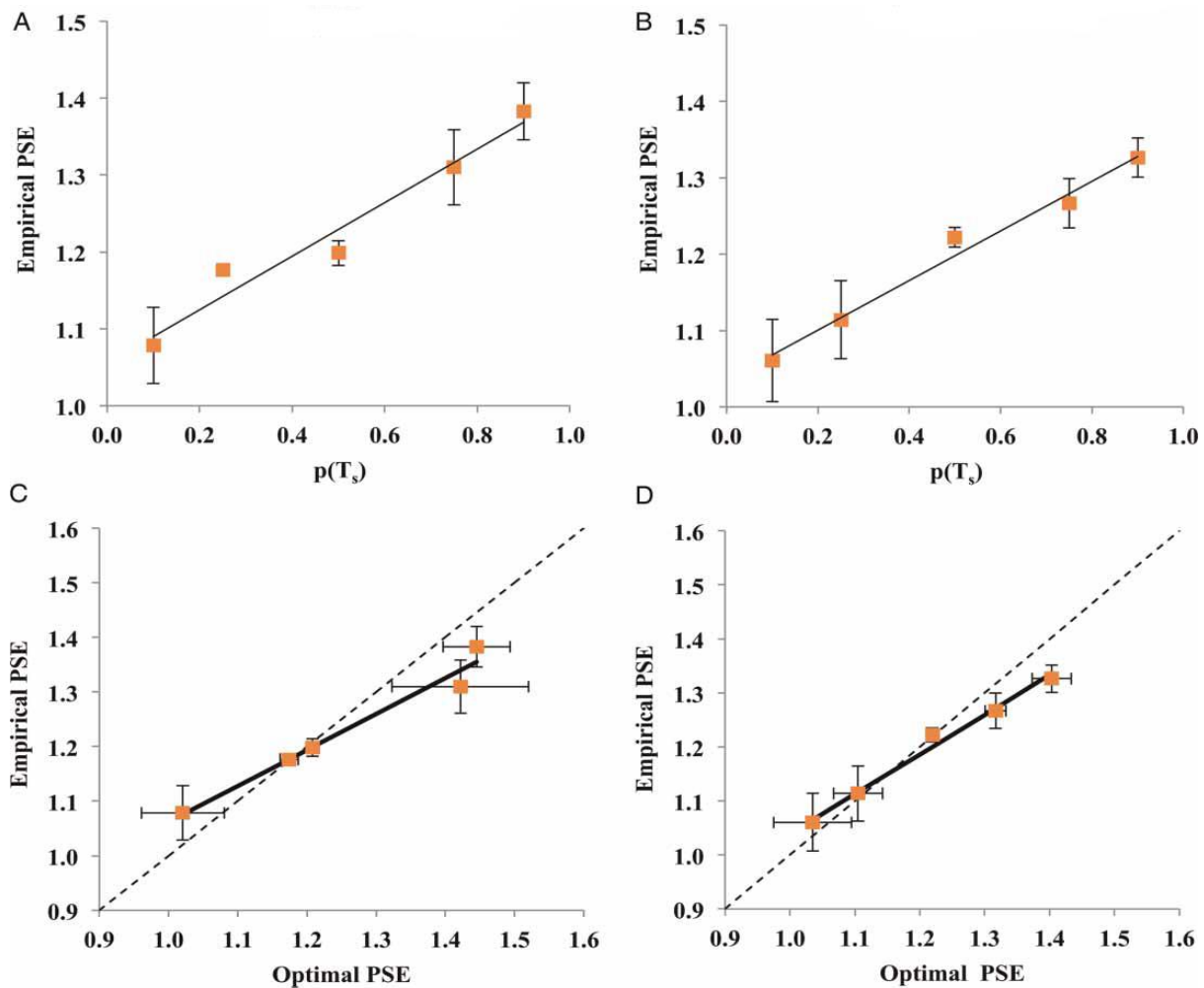
Figure 4. Average empirical PSEs as a function of short reference duration probabilities for Group 1 (A) and Group 2 (B); thin line is the best-fit linear regression line. Average empirical PSEs as a function of average optimal PSEs separately for different reference probability conditions for Group 1 (C) and Group 2 (D). Bold solid lines are the best-fit orthogonal regression lines. Diagonal dashed thin lines are the identity line. Error bars stand for SEM.

Finally, we calculated the AIC scores for the individual participants' choice

proportions under the best fitting and the optimal cumulative Gaussian distributions for the

corresponding exogenous probability conditions (using the same CV estimate). The median

ΔAIC scores were 9.59 and 12.96 favoring the best-fitting Gaussian parameters over the

optimal model parameters for Groups 1 and 2, respectively. When the empirical choice

proportions were evaluated under the best-fitting and the optimal cumulative Gaussian distributions calculated for the exogenous probability condition tested in the other session, the median ΔAIC scores rose to 20.61 and 22.28 for Groups 1 and 2, respectively. These results suggest that the empirical behavior was closer to the optimal strategy computed for the exogenous probability conditions under which the choice behavior was actually observed.

The comparison of the CV estimates between four different unequal probability conditions (between-group comparison) did not reveal a significant overall difference in either Group 1 (χ^2 (3, $N = 24$) = 4.19, $p = 0.24$) or Group 2 (χ^2 (3, $N = 24$) = 0.59, $p = 0.90$). The within-group comparison of CV estimates between unequal and the corresponding equal probability conditions did not reveal any significant differences either (all ps > 0.34).

f. Expected gains. The expected gain was calculated for the empirical PSEs, levels of endogenous timing uncertainty, reference probabilities, and payoff matrix and compared with the maximum possible expected gain (MPEG) calculated separately for each participant given his or her level of timing uncertainty and the corresponding task parameters. Figure 5(A) and (B) demonstrates the proportion of MPEG for possible target PSEs separately in five different reference probability conditions (calculated for average CVs) for Groups 1 and 2, respectively. Visual inspection of this figure points at nearly optimal performance of the participants. The analysis of individual participants' data corroborated this observation; the participants earned 99, 99.8, 99.9, 99, and 99% of the MPEG (median) in Group 1, and 99.6, 97, 98, 96, and 97% of the MPEG (median) in Group 2 for increasing short reference probabilities, respectively.
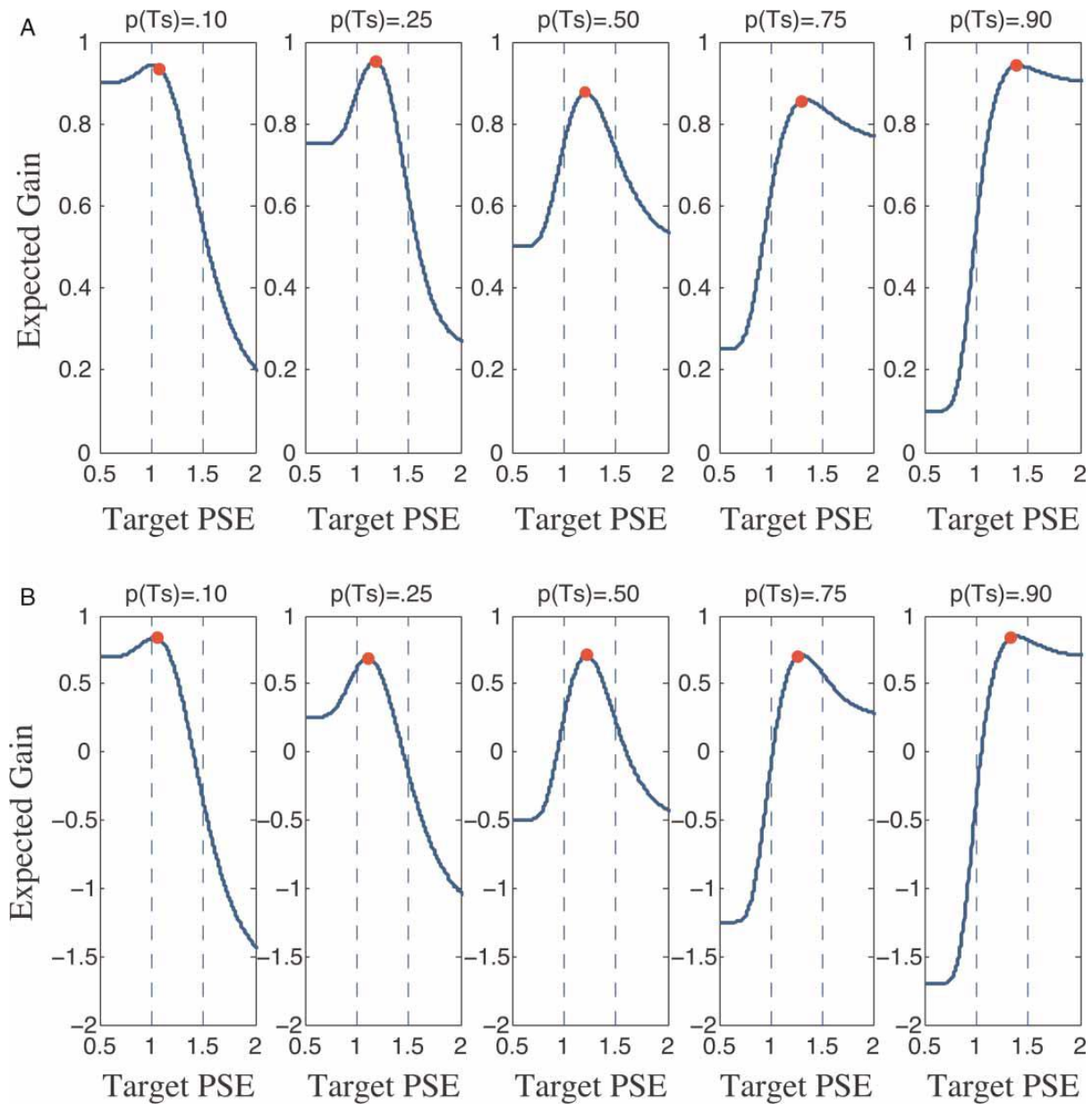
Figure 5. Expected gain as a function of possible target PSEs in five different probability conditions for Group 1 (A) and Group 2 (B). Expected gains were calculated using average empirical CV values estimated from the corresponding probability conditions and groups. Vertical dashed lines denote the short and long reference durations. The locations of the red filled circles show the average target PSE separately for different exogenous probability conditions.

In a second set of analyses, the gain expected from random categorization of durations was considered as the minimum gain that can be attained; in this latter case the proportion of maximum possible expected gain was computed as (Expected gain — Minimum gain)/(MPEG — Minimum gain). The results from this second set of analyses were

comparable with values gathered from the initial set of analyses: 99, 99.5, 99.7, 98, and 99% (median) for Group 1 and 99.8, 98, 99, 97, and 98% (median) of the MPEG for Group 2 for increasing short reference probabilities. Note that this second way of calculating the proportion of MPEGs constitutes a more stringent approach for Group 1 whereas it is a more lenient approach for Group 2 (due to the negative gain associated with random responding).

There were no significant differences between the proportion of MPEG between equal and unequal probability conditions (within-group comparison) for either lenient or stringent approaches in Group 1 (both ps > 0.17) or in Group 2 (both ps > 0.49). Then what participants would have earned in the equal reference probability condition if they adopted their unequal reference probability condition strategy (i.e., PSE), and in the unequal reference probability condition if they adopted their equal reference probability condition strategy were computed. It was found that the participants would have earned significantly less if they had adopted their equal reference probability condition strategy for unequal reference probability conditions and vice versa: $t(23) = 4.61$, $p < .001$ and $t(23) = 3.96$, $p < .001$, respectively for Group 1; $t(23) = 2.55$, $p < .05$ and $t(23) = 3.63$, $p < .01$, respectively for Group 2 (within-group comparison). These results point at the adaptive value of the changing temporal decision strategies in response to changing probabilistic information in these specific task conditions.

f. Response times. Visual inspection of Figure 6(A) and (B) suggests that average RTs for short categorizations (short categorization RTs) sped up with increasing short reference probability in the absence of any apparent changes in the long categorization RTs. There was a significant relationship between short categorization RTs and short reference probability, $F(1,3) = 12.71$, $p < .05$, $R^2 = .85$ in Group 1 and $F(1,3) = 10.62$, $p < .05$, $R^2 = .78$ in Group 2, but this relationship did not hold for long categorization RTs, $F(1,3) = .36$, $p = 0.59$, $R^2 = .11$ in Group 1 and $F(1,3) = 2.76$, $p = 0.20$, $R^2 = .48$ in Group 2.
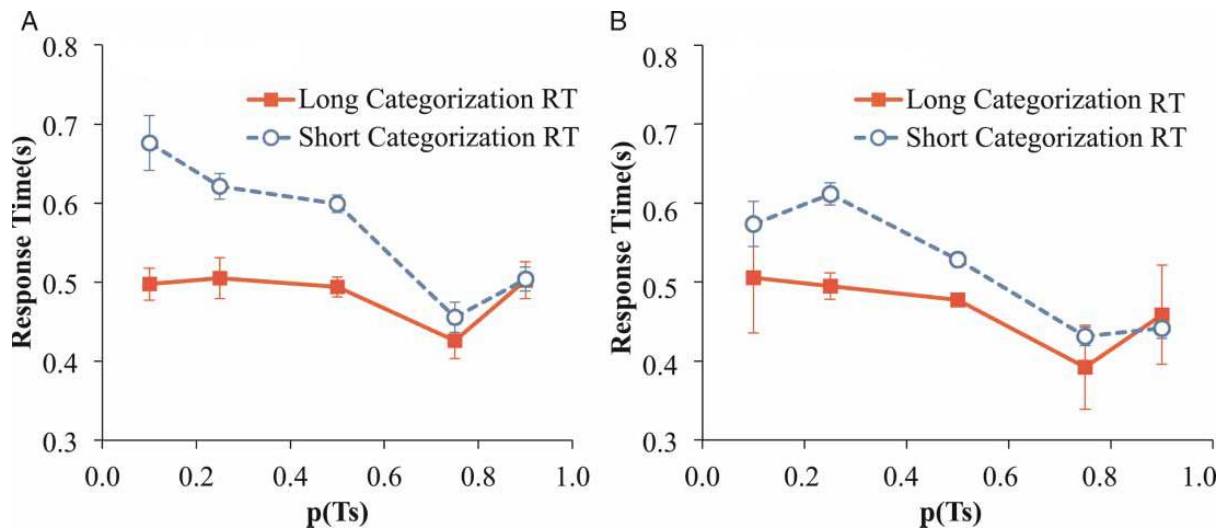
Figure 6. Average short and long categorization response times (mean response times pooled across different test durations per participant) separately for different probability conditions in Group 1 (A) and Group 2 (B). Error bars stand for SEM.

The between-group comparison of the short categorization RT-long categorization RT difference score between different unequal probability conditions revealed a significant overall difference, $\chi^2(3, N=24) = 16.90$, $p < .001$, $\eta^2 = .57$ for Group 1 and $\chi^2(3, N=24) = 18.69$, $p < .001$, $\eta^2 = .84$ for Group 2. Pair-wise comparisons of these values revealed significant differences between all unequal probability condition pairs but $p(T_S) = .10 - .25$ and $p(T_S) = .75 - .90$ pairs (all ps < 0.05) in Group 1, and $p(T_S) = .10 - .25$ pair (all ps < 0.05) in Group 2 (Holm-Bonferroni corrected). There were no significant differences between the corresponding equal probability conditions ($p = 0.97$ for Group 1 and $p = 0.62$ for Group 2, between group comparisons). Within-group pairwise comparisons of short categorization RT-long categorization RT differences in unequal and the corresponding equal probability conditions revealed significant differences only for $p(T_S) = .75$ and $p(T_S) = .90$ conditions in Group 1 and for $p(T_S) = .10$ and $p(T_S) = .25$ conditions in Group 2 (all ps < 0.05). There were no significant differences left after the Holm-Bonferroni correction. The within-group comparison of the left- and right-hand RTs in the visual discrimination task did not reveal a significant difference, $t(23) = .43$, $p = 0.68$ for Group 1 and $t(20) = .35$, $p = 0.73$ for Group 2. Thus, differences between short and long categorizations RTs cannot be accounted for simply

by faster right-hand response times. Short categorization RTs slowed down, whereas long categorization RTs sped up with longer durations (see Figure 7(A) and (B)), suggesting that correct categorization RTs (e.g., comparing for the equal probability condition) were faster than incorrect RTs. The statistical results of linear regression of short and long categorization RTs on stimulus durations are summarized in Table 1.
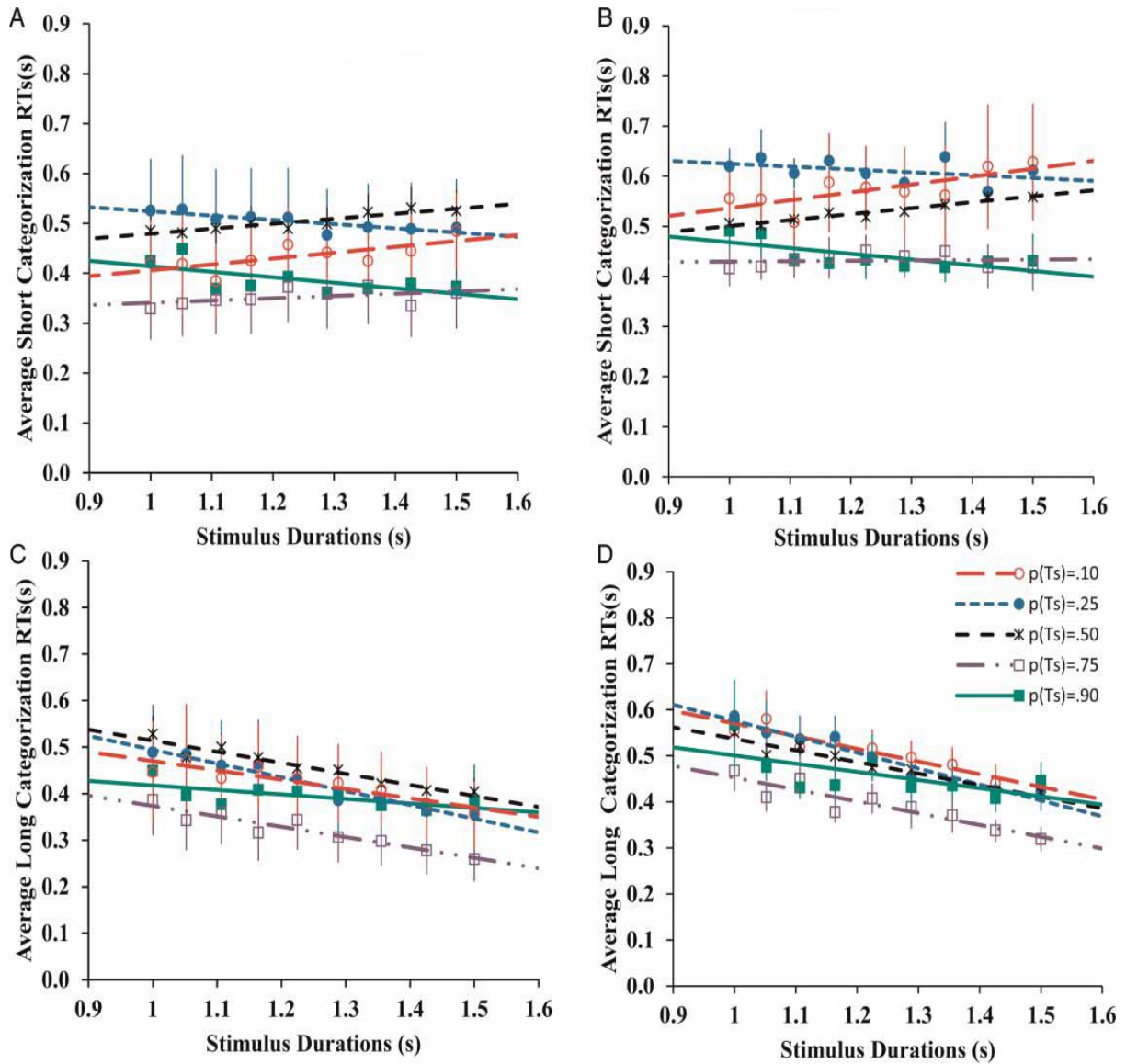
Figure 7. Average short (A & B) and long categorization (C & D) response times as a function of probe durations separately for five different probability conditions for Group 1 (A & C) and Group 2 (B & D). Lines are best-fit linear regression lines. Error bars on the graph stand for SEM.

Table 1. The statistical results of linear regression of short and long RTs on stimulus durations (compare to Figure 7)

$F(1,7) =$		Group 1	Group 2
$p(T_S) = .10$	Short RT	**7.15, $p < .05$, $R^2 = .51$**	**8.75, $p < .05$, $R^2 = .56$**
	Long RT	**33.60, $p < .001$, $R^2 = .83$**	**75.62, $p < .001$, $R^2 = .92$**
$p(T_S) = .25$	Short RT	**15.67, $p < .01$, $R^2 = .69$**	1.52, $p < .26$, $R^2 = .18$
	Long RT	**111.77, $p < .001$, $R^2 = .94$**	**118.22, $p < .001$, $R^2 = .94$**
$p(T_S) = .50$	Short RT	**34.18, $p < .001$, $R^2 = .83$**	**84.18, $p < .001$, $R^2 = .92$**
	Long RT	**77.83, $p < .001$, $R^2 = .92$**	**95.34, $p < .001$, $R^2 = .93$**
$p(T_S) = .75$	Short RT	2.06, $p < .19$, $R^2 = .23$	0.06, $p < .81$, $R^2 = .01$
	Long RT	**55.87, $p < .001$, $R^2 = .89$**	**33.65, $p < .001$, $R^2 = .83$**
$p(T_S) = .90$	Short RT	*4.86, $p < .06$, $R^2 = .41$*	**7.25, $p < .05$, $R^2 = .51$**
	Long RT	*5.40, $p < .053$, $R^2 = .44$*	*4.41, $p < .07$, $R^2 = .39$*

Note: Significant relations are indicated by bold font and trends are indicated by italic font for ease of visual inspection.

3. Discussion

The temporal discrimination behavior of human participants was tested in the temporal bisection task with different reference duration probabilities (exogenous probability) and payoff matrices (with penalty vs. without penalty for errors) and their performance was evaluated within the framework of Statistical Decision Theory that incorporated the participants' endogenous timing uncertainty along with the experimentally manipulated probabilistic and gain-related task parameters. Endogenous timing uncertainty was estimated from the participants' choice proportions while exogenous probabilities were manipulated by changing the relative frequencies of the reference durations. Through these analyses, the optimality of temporal bisection behavior was assessed for the first time and in its full complexity.

The participants shifted their bisection point leftward with decreasing and rightward with increasing short reference probabilities. In other words, the participants were more likely

to categorize a given duration as long in the former and as short in the latter case. These findings are consistent with those reported in Jozefowiez, Polack, Machado, and Miller (2014), who also manipulated the relative frequency of short and long reference durations in a variant of the temporal bisection task. However, the observed temporal discrimination performance was not evaluated within the framework of optimality in that study. Importantly, observed changes in temporal strategies in response to changing probabilities in the current study nearly tracked optimality and significantly increased the expected gain in this task. By adjusting their choice behavior, the participants earned nearly the MPEG they could attain given their endogenous timing uncertainty level (i.e., CV), experienced exogenous probability (i.e., $p(T_S)$), and the payoff matrix. Note that optimality in this task did not only depend on the exogenous probabilities but also on the level of the participants' endogenous timing uncertainty (depicted in Figure 2, see the Optimality analysis section above).

The relationships depicted in Figure 2 highlight a ubiquitous feature of temporal decision-making; time-based decisions are by default subject to timing uncertainty and its psychophysical properties, integral elements of human and non-human animal interval-timing ability. As the participant aims at an earlier bisection point (switching from a short to a long categorization state), the absolute level of timing noise (i.e., standard deviation) that the participant is confronted with is effectively reduced. On the other hand, in the current task this tendency might be counteracted by the higher probability of short target intervals if manipulated as such in the task condition. This is why the optimal target bisection points are farther apart between the different exogenous probability conditions for higher levels of timing imprecision. Thus, temporal bisection task as utilized in this work and its optimality analysis are closely linked to the interval timing ability.

These findings overall suggest that humans can adjust their temporal bisection decisions in a normative fashion in response to changing task-relevant probabilistic

information while taking account of the level of their own endogenous timing uncertainty. Note however that although empirical PSEs followed the optimal PSEs closely, this relationship was not perfect (see Figure 4). Specifically, the participants deviated from optimality when the optimal PSEs were very close to the short or long reference durations. This might be due to the suboptimal tendency of humans to avoid aiming at a point outside the range of reference durations or at durations that delimit the range even when they lead to reward maximization. Subtle deviations from optimality due to similar tendencies have been previously observed in motor planning studies. For instance, Trommershäuser, Gepshtein, Maloney, Landy, and Banks (2005) reported that when the optimal target motor end-point fell outside the reward region, the participants preferred not to aim for it, whereas their motor end-points were optimal when the optimal target was inside the reward region.

Alternatively, the participants in this study might have simply made the short and long choices differentially without taking account of their timing uncertainty. Figures 2 and 5 on the other hand suggest that without integrating the level of timing uncertainty into their decisions, the participants would have suffered from substantial loss of reward earned particularly in Group 2. The evaluation of expected gains however showed that the participants nearly maximized their gain. The nearly optimal temporal decision performance of the participants is consistent with those of earlier studies conducted with humans and non-human animals. For instance, Balcı et al. (2009) and recently Kheifets and Gallistel (2012) observed nearly optimal performance of humans and mice in the switch task that also entailed taking account of the endogenous timing uncertainty, in addition to exogenous probabilities and payoffs for reward maximization. On the other hand, distinct from the temporal bisection task where the participants indicate their temporal judgments after the cessation of the timing stimulus (as requested in this work), the switch task required the participants to indicate their temporal judgments continuously during the timing stimulus.

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Despite these procedural differences, the decision processes that take place during timing stimulus and that underlie temporal bisection resemble those that underlie switching decisions. For instance, Machado and Keen (2003) found that in the bisection task pigeons moved from the location associated with short to the other location associated with long reference duration typically when the stimulus duration approached and exceeded the PSE. This pattern closely resembled the typical response pattern observed in the switch task (e.g., Balcı et al., 2008). On the other hand, different from the switch task, the categorizations in the temporal bisection task should also rely on post-stimulus decision processes. To this end, response times provide valuable clues regarding the contribution of prospective and retrospective components of temporal bisection performance to temporal choice behavior and the relation between them (Balcı & Simen, 2014; Rodríguez-Gironés & Kacelnik, 1998).

For instance, observed patterns of changes in short and long categorization RTs as a function of test durations (Figure 7) overall suggest that at least the post-stimulus decisions in the temporal bisection task might rely on noisy evidence accumulation (e.g., Balcı & Simen, 2014; Ratcliff, 1978, 2001; Ratcliff & McKoon, 2008; Ratcliff & Rouder, 1998). Short categorization RTs slowed down whereas long categorization RTs sped up with longer test durations, namely RTs were faster for correct compared to "erroneous" categorizations. Combined with the observed choice proportions, this pattern predicts longer overall RTs for durations that are farther away from the two reference durations (or closer to the PSE). This particular pattern in turn suggests that the post-stimulus rate of evidence accumulation might be determined by some distance metric between the elapsed time and the criterion set between the reference durations (e.g., Allan, 2002; Balcı & Gallistel, 2006; Balcı & Simen, 2014; Wearden & Ferrara, 1995). Within this framework, the rate of evidence accumulation would be low for test durations closer to the PSE, high in one direction for test durations

closer to the short reference duration, and high in the opposite direction for test durations closer to the long reference duration.

Response time patterns further implied the contribution of prospective components to the temporal bisection performance. Specifically, long categorization RTs were reliably faster than the short categorization RTs (for all probability conditions except for when $p(T_S) = .90$). Faster RTs for long categorizations were expected (at least when $p(T_S) \leq p(T_L)$) due to an asymmetry in the nature of short and long categorizations. If the participants also compared elapsing time to a criterion during the timing stimulus and decision processes had already favored a long categorization prior to the cessation of this stimulus, then the participants could commit to these decisions from thereon. In those cases, the participant would simply wait for the cessation of the timing stimulus to indicate the decision that had been already made during the timing stimulus (note that in this task the participants were not allowed to respond during the stimulus). On the other hand, short categorizations cannot benefit from these response time gains, as the participants should not commit to short categorizations prior to the stimulus cessation (except when $p(T_S) = 1$); the current stimulus can last longer and eventually favor a long categorization. Note that if the participant had not made the long categorization during the timing stimulus, she or he would have to rely on post-stimulus evidence accumulation to reach a categorization decision, and the frequency of these cases would decrease with increasing test duration.

The asymmetry mentioned above has been recently demonstrated in a temporal generalization task (Klapproth & Müller, 2008; Klapproth & Wearden, 2011). In this task, the participants are familiarized with a standard time interval and asked to judge if an experienced time interval is the same as or different to the standard. The resultant proportion of same judgments as a function of test durations results in a generalization gradient that peaks at the standard duration. Klapproth and colleagues tested human participants under two

conditions; accuracy and speed. In the speed condition, they were asked to make their decisions as soon as possible, whereas in the accuracy condition, they were allowed to take their time. Different from the current study, they allowed the participants to respond prior to the cessation of the timing stimulus and measured response times starting from the onset of the timing stimulus. In both studies, they observed that under speeded conditions the response times for same judgments increased linearly with the to be-judged time interval whereas the response times for different judgments increased until the standard duration and stayed stable from there on. These observations provide support for the claim that the participants are indeed engaged in decision-making during the timing stimulus and thus they do not exclusively rely on post-stimulus decisions. Different from the studies by Klapproth and colleagues, the participants of the current study were not allowed to indicate their decisions prior to the cessation of the stimulus, and response times were indexed as the time elapsed between stimulus offset and the response. If the participants were allowed to respond during the stimulus, it would be likely to observe a similar pattern for long judgments. Further studies are needed to test this interesting prediction.

It could be argued that the participants did not pay attention to the time and simply chose the interval that was most frequent (especially in conditions with .9 probabilities). If this was the case, one would expect the choice function to be a flat line either at $p(\text{long}) = 0$ or $p(\text{long}) = 1$, depending on the probability of reference durations. A subgroup of participants indeed exhibited loss of temporal control over their choice behavior in a similar task utilized by Jozefowiez et al. (2014), suggesting that those participants did not integrate temporal processing into their choice behavior. On the other hand, all of the participants in the current study exhibited a good level of temporal control over their choice behavior (even in extreme probability conditions), which entailed reliance on temporal processing along with the probabilistic information.

The reward-maximization-based approach to temporal bisection performance also suggests a resolution to the controversy regarding the location of the PSE (Balcı, Freestone, et al., 2011). Temporal bisection task is typically utilized with equal reference duration probabilities in the literature and these studies report PSEs to be closer to the geometric mean of the reference duration in non-human animals (e.g., Church & Deluty, 1977) and closer to the arithmetic mean of the reference durations for humans (e.g., Balcı & Gallistel, 2006). The location of the PSE has been claimed to have implications regarding the nature of subjective time scale (Montemayor & Balcı, 2007; Yi, 2009). However, the reward-maximization approach to temporal bisection performance suggests that the location of the PSE might simply be a function of reward maximization, which is modulated due to different levels of timing uncertainty. Since humans have lower timing uncertainty compared to non-human animals, human PSEs are indeed expected to be closer to the arithmetic mean (see Figure 2 middle panel).

Reward maximization in a temporal bisection task requires the associated choice behavior to also be independently sensitive to differences between the values of options in terms of associated reward magnitudes (e.g., Balcı et al., 2009). Findings from a number of earlier studies using variants of a temporal bisection task with pigeons and rats confirmed this prediction (Bizo & White, 1994, 1995; Guilhardi, MacInnis, Church, & Machado, 2007). Specifically, in these studies animals switched from the richer option (that predicted a reward earlier in the trial) to the poorer option (that predicted a reward later in the trial) later in the trial when options predicted a reward according to different variable-interval schedules. Likewise, they switched from poorer option (that predicted a reward earlier in the trial) to the richer option (that predicted a reward later in the trial) earlier in the trial. Testing the effects of similar payoff manipulations in temporal bisection tasks and the optimality analysis of the resultant choice behavior is needed.

As mentioned earlier, the current findings corroborate those reported in Jozefowiez et al. (2014), who also tested the effect of reference duration probabilities on temporal bisection choice behavior. However, different from Jozefowiez et al. (2014), this study extends the investigation of the effect of reference duration probabilities on temporal bisection behavior in novel directions to include: 1) a reward-maximization-based approach to the modulation of choice functions that incorporates psychophysical properties of interval timing; 2) testing temporal bisection behavior with different payoff matrices; and 3) the analysis of response time modulation in addition to choice proportions. There are also noteworthy procedural differences between the two studies, such as the lack of feedback for the categorization of reference durations, use of drastically fewer trials for testing, and use of fewer intermediate durations in Jozefowiez et al. (2014). Possibly due to the combination of these minute procedural details, a non-negligible proportion of the participants in Jozefowiez et al. (2014) failed to exhibit temporal control over their choice behavior.

One of the relevant issues that relate to the current findings in terms of optimal choice behavior regards the generalizability of these findings to decisions about other quantities. Although further empirical tests are needed to address this issue, it is possible that similar effects apply to other domains that are subject to well-structured representational noise characteristics. For instance, non-verbal numerosities as another magnitude-based representation are also represented with scalar variability (e.g., Gallistel & Gelman, 1992; Platt & Johnson, 1971; Whalen, Gallistel, & Gelman, 1999). The temporal bisection task can also be utilized with numerosities. In such a task, the judgments would take a form closer to the "fewer" vs. "more" option. The prediction is that in such tasks endogenous noise characteristics along with exogenous probabilities can also be integrated into the categorization decisions about numerosities. Previous data from rats suggest that endogenous

noise might indeed be a factor that affects decisions about numerosities (Mechner, 1958). The test of any other domain (e.g., distance) should also take account of the corresponding representational noise characteristics while evaluating the empirical performance within the framework of optimality. These would constitute good follow up tests of this theoretical approach and its generalizability.

Study 2

1. Methods

a. Subjects.

Humans. Ten adult participants (5 females and 5 males; $M_{age} = 21.10$, $SD_{age} = 0.55$) took part in this study after providing informed consent. Participants were recruited through a publically available daily newsletter (KUDaily) published on Koç University website. Monetary compensation was provided based on each participant's performance. Total payments ranged between 55-86 TL (~20-32 USD). All procedures were approved by the Koç University Ethical Committee on Human Research.

Mice. Twenty experimentally naive male C57BL/6J mice were used in the study. One mouse was discarded from the experiment due to health problems. Mice were approximately 10 weeks old upon arrival. They were kept in individually ventilated cages lit on a 12:12 h photoperiod. The experimental sessions were conducted during the light period. During the experimentation, mice were kept at about 85% of their baseline weight through caloric restriction. Each mouse was weighed daily and fed 30 minutes after the completion of the test session. Mice had ad-lib access to water in their home cages. Water was removed from the cage one hour prior to the session. All procedures were approved by the Koç University Animal Research Local Ethics Committee.

b. Stimuli and apparatus.

Humans. The temporal stimuli displays were generated and the responses were recorded in MATLAB on a Macintosh computer, using the Psychophysics Toolbox extensions (Kleiner et al., 2007).

Mice. Experiment was conducted in eight operant chambers (Med Associates, ENV-307W: 21.6 cm x 17.8 cm x 12.7 cm) located inside ventilated and sound-attenuated boxes. All operant chambers were equipped with three illuminable feeding hoppers with liquid dippers (ENV-302RW), and each dipper cup was able to deliver 0.1 cc liquid reinforcement (Isosource Standard Nutrition Product) in the associated hopper. These three illuminable hoppers were located along one of the sidewalls of the chamber and each was equipped with a head entry detector (ENV-302HD). Another hopper located at the middle panel of the opposing wall was used for mice to initiate the trials. White-noise generator (ENV-230) signaled the auditory stimuli. Before each session started, a cooling fan was turned on for ventilation and eliminating any other sound effects. Med-PC IV Software (Med Associates) was used to control the experimental protocol. The event times were recorded in time-event format with a resolution of 10 ms.

c. Procedure.

General procedure. Three types of trials were used: short trials, medium trials, and long trials. In each trial type, a temporal stimulus (visual stimulus for humans and visual/auditory stimuli for mice) was presented until the target duration elapsed. There were three response locations, each of which was associated with a different target duration. In each trial, subjects had to respond at the correct location for the corresponding trial type at the end of the target interval (or after the target interval, for mice) in order to receive reward. As the trial type was not signaled by a discriminative stimulus, the expected response pattern

was 1) waiting at the short location until the short interval was judged to have elapsed, 2) switching to the second location associated with the medium delay-to-reward if the reward was not received at the current location, and 3) switching to the third location associated with the long delay if no reward was presented at the second location by the time the medium interval was judged to have elapsed.

In the short trials, subjects could only make an error if they switched earlier than the duration of the short interval. Subjects could make two types of errors in medium trials: one by either failing to have switched to the hopper associated with this trial type by the end of the target interval, and second by making a switch from the medium to the long interval location before the medium duration elapsed. Lastly, in the long trials, the subjects could miss the reward if they had not switched to the long location by the end of the long interval. Correct responses were reinforced for both humans and mice. For incorrect responses, mice only missed the reward whereas humans received point penalty. In the study, the probability of different trial types was manipulated across sessions (for humans) or phases (for mice) in order to investigate its possible modulatory effect on switch latencies.

Humans. The target durations were 2, 3, and 4.5 s for short, medium, and long trials, respectively. Three neighboring gray squares were presented on the computer screen. Each square was associated with a different delay to reward availability: The left-most square was associated with the short duration, the middle square was associated with the medium duration, and the right-most square was associated with the long duration. Each trial started with the presentation of the three gray squares and a red frame around the left-most square, which subjects moved in order to indicate their decisions. Participants were asked to catch the reward by moving the red frame between the squares. They could move the frame from the left-most to middle, and from the middle to right-most squares by pressing the keys 'B' and 'N', respectively. The participants gained reward if the frame was at the correct location by

the end of the active trial duration. Otherwise, they lost a point in that trial. Correct responses resulted in a brief beep sound while incorrect responses resulted in a brief buzzer sound. At the end of each 20th trial, subjects could see the total score they had accrued and take a break.

The experiment was comprised of five daily sessions, each consisting of 420 trials. In each session, the participants were tested in a different probability condition. In the first session, each participant was tested in the equal reference duration probability condition $(p(T_S) = .33: p(T_M) = .33: p(T_L) = .33)$. This was the practice session in which the baseline performance was established. There were four unequal probability conditions: (1) the lowest probability for the short duration $(p(T_S) = .17: p(T_M) = .415: p(T_L) = .415)$, (2) the lowest probability for the long duration $(p(T_S) = .415: p(T_M) = .415: p(T_L) = .17)$, (3) the highest probability for the short duration $(p(T_S) = .66: p(T_M) = .17: p(T_L) = .17)$, (4) the highest probability for the long duration $(p(T_S) = .17, p(T_M) = .17, p(T_L) = .66)$. The order of the unequal probability conditions was counterbalanced across participants. As the first session was treated as the practice session, all participants, except for one, were tested in the equal probability condition in one more (final) session.

Mice. At the beginning of each trial, the light in the control hopper was turned on. Mice initiated the trials with a nose poke into this illuminated hopper. This requirement ensured that mice were at a fixed location at the trial onset. An inter-trial interval of a fixed 30 s plus a variable interval sampled from an exponential distribution with a mean of 30 s was used. All sessions lasted 60 min.

Training. In the training phase, the target durations for short, medium, and long trials were 3, 9, and 27 s, respectively. All trial types were presented with equal probability. When the mouse started a trial, three feeding hoppers were illuminated and the white noise was initiated. The white noise was terminated after the target interval elapsed and reward was

presented in the correct location for that trial type irrespective of the subjects' response (autoshaping). The location-duration pairing for the shortest and longest durations was counterbalanced across subjects.

The expected response pattern was a sequential timed switching behavior: first switching from the short to the medium location when the short latency was judged to have elapsed without reward delivery (in the medium and long trials), and then switching from the medium to the long location when the medium duration was judged to have elapsed without reward delivery in the long trials. When a mouse exhibited this response pattern in 75% of the long trials in three consecutive sessions, the testing phase was completed.

Mice were tested in two batches. Subjects in the second batch (seven mice) were tested until this criterion was met. The total number of sessions ranged between 10- 28. In the first batch (13 mice), the animals that had not met the criteria by the end of 15 sessions (eight mice) were assigned to a new five-session-long autoshaping procedure, where only the active hopper was illuminated in a given trial. In this way, mice were signaled the correct location for the corresponding trial type. After completing five sessions, these mice were again assigned to the previous training procedure (the learning criterion was held the same). Two mice met the criteria within four sessions and were moved to the next phase. The remaining six mice that failed to reach the criteria were assigned to the next phase after completing 14 sessions.

Testing phase 1. During the testing phase, the reward was delivered only if the first response at or after the offset of the target interval was emitted at the correct hopper. The hopper lights remained on until a head entry was detected in any of the three hoppers. The testing phase lasted for at least 33 sessions. The criteria for completing this phase were determined as exhibiting sequential timed switching behavior in at least 75% of the long trials

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and attaining at least 95 % of the maximum possible expected gain (see *Optimality Analysis*) in five successive sessions.

Three subjects failed to meet the criteria as they exhibited low switch ratios by the end of the 27th session. For these mice, the procedure was modified: the trials were terminated if the animals were not responding by the end of the target duration. This training aimed to induce the timed switching behavior. The criteria for proceeding to the next phase were held the same (exhibiting timed switching behavior in at least 75% of the long trials and attaining at least 95 % of the maximum possible expected gain in five consecutive sessions). These mice met the criteria within at least 10 and at most 21 sessions.

After mice completed the testing phase, the durations were decreased to 3, 6, and 12 s, constituting a lower ratio. After 10 sessions, the durations were further decreased to 4, 6, and 9 s (constituting the same ratios with the human group). All subjects were tested with these durations for 13 sessions. Upon completion of this phase, one mouse was discarded from the study due to health problems.

Testing phase 2. In Phase 2, subjects were divided into two groups each of which was assigned to an unequal probability condition. Group 1 was tested in $p(T_S) = .2$: $p(T_M) = .2$: $p(T_L) = .6$ condition and Group 2 was tested in $p(T_S) = .6$: $p(T_M) = .2$: $p(T_L) = .2$ condition. This phase lasted for 13 sessions.

Testing phase 3. In Phase 3, the probability conditions were reversed for the two groups. Thus, Group 1 was tested in $p(T_S) = .6$: $p(T_M) = .2$: $p(T_L) = .2$ condition, whereas Group 2 was tested in $p(T_S) = .2$: $p(T_M) = .2$: $p(T_L) = .6$ condition. The mice were tested for 13 sessions in this phase.

d. Data analysis. Human data for all five different probability conditions collected in

different sessions were used in the analyses. Participants were tested with the equal probability condition in the first and last sessions. For this probability condition, the data from the last session was included in the analyses. For one subject who was not tested in the equal probability condition twice, the data from the first session was used. For mice, different trial type probabilities were manipulated across phases. For each phase, data pooled across the last five sessions were used in the analyses.

The main units of analysis were the first and the second switch latencies observed in the long trials. Only the long trials were included in the analysis because they constitute the ideal/non-censored conditions for observing the sequence of temporal decisions. The latency at which the subjects shifted from the short location to the medium location was recorded as the first switch latency, whereas the latency at which the subjects shifted from the medium location to the long location was recorded as the second switch latency. In order to record a second switch latency, a first switch was required in the long trials. The trials with no switching behavior were eliminated from the analyses as they did not reflect task-representative behavior and/or task engagement.

Cumulative exponential Gaussian mixture distribution functions were fit to the switch latencies using the least squares method. The best fitting Gaussian parameters were treated as the timing indices of the task-representative timed responses; the mean was treated as the target switch latency and the coefficient of variation ($CV = \sigma/\mu$) of the obtained distributions was treated as the index of primarily timing uncertainty.

Repeated-measures ANOVAs were run to compare the mean first and second switch latencies and CV values across different probability conditions. The Greenhouse-Geisser correction was used when the sphericity assumption was violated. The alpha level was set to .05 (two-tailed) for all of the statistical analyses. Where appropriate, pair-wise

comparisons were conducted using paired-samples *t*-tests. The Holm-Bonferroni correction was applied to adjust the *p* values for multiple comparisons.

Optimality analysis. The expected gain in this task was dependent on the level of endogenous uncertainty, the probability of different trial types, and the payoffs associated with correct/incorrect responses. In order to find the optimal target latencies separately for the first and second switches, the expected gain was calculated for each subject that would result from targeting different hypothetical switch latencies (given its CV), using the Equation 1 (see Optimality Analysis for Study 1). Note that, every parameter in the formula associated with short notation (T_S, $p(T_S)$, $g(T_S)/g(\sim T_S)$) stands for the shorter of a pair, and associated with long notation (T_L, $p(T_L)$, $g(T_L)/g(\sim T_L)$) stands for the longer of a pair for the first and second switches.

2. Results

e. Human data. Figure 8 shows average normalized first and second switch latencies for different probability conditions. A one-way repeated-measures ANOVA was conducted to investigate the effect of probability condition separately on the first and second switch latencies. The results revealed a significant difference in the first switch latencies across different probability conditions, $F(4, 36) = 9.78$, $p < .001$, $\eta_p^2 = .52$. The results of the pair-wise comparisons (Holm-Bonferroni corrected) are presented in Table 2. The difference between all pairs was in the expected direction; participants switched earlier when the probability of the short trial was low and later when this probability was high.
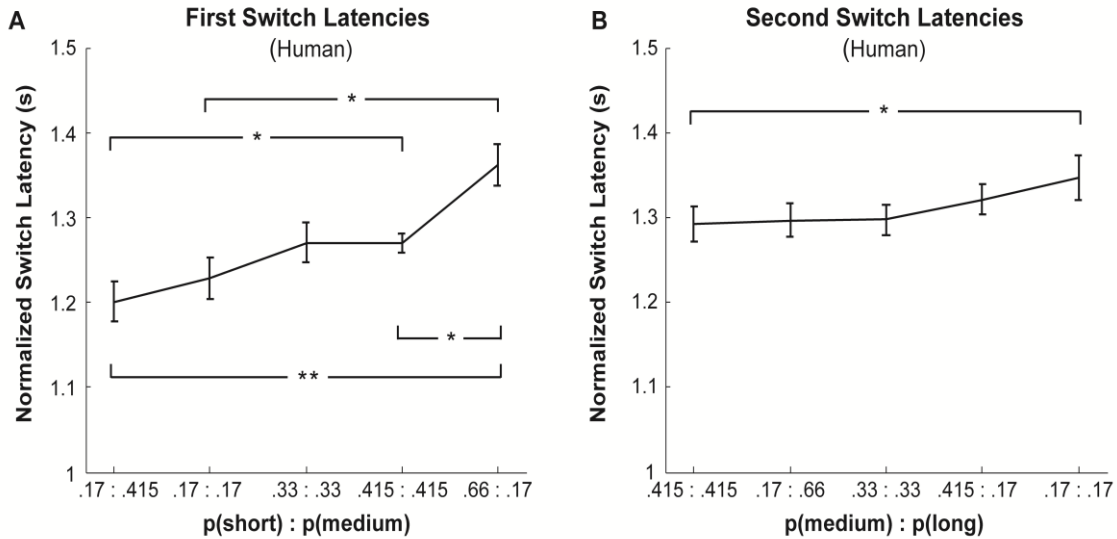
Figure 8. First (A) and second (B) mean switch latencies (normalized by 2 and 3 s, respectively) for different probability conditions (*p < 0.05, **p < 0.01).

Table 2. The paired-samples t-test comparisons of the mean first switch latencies between different probability conditions denoted in bold (human data)

	M	*SD*	*t(9)*	*p*
p(T_S) = .66 : p(T_M) = .17	**2.72**	**0.15**		
p(T_S) = .17 : p(T_M) = .415	2.40	0.15	5.29	.01
p(T_S) = .17 : p(T_M) = .17	2.46	0.16	3.72	.04
p(T_S) = .415 : p(T_M) = .415	2.54	0.07	3.70	.04
p(T_S) = .17 : p(T_M) = .415	**2.40**	**0.15**		
p(T_S) = .415 : p(T_M) = .415	2.54	0.07	-3.64	.04

The same analyses were conducted to compare second switch latencies across

different probability conditions. The results revealed a significant effect of trial type

probability, $F(4, 36) = 4.69$, $p = 0.004$, $\eta_p^2 = .34$. Follow-up pair-wise comparisons indicated

that there was a significant difference only between $p(T_M) = .415: p(T_L) = .415$ ($M = 3.88$,

$SD = 0.20$) and $p(T_M) = .17: p(T_L) = .17$ ($M = 4.04$, $SD = 0.25$) conditions ($p = 0.03$, Holm-

Bonferroni corrected).

In order to investigate particularly whether participants treated the probabilities within

pairs locally or globally, one can evaluate the pair-wise comparisons of the conditions where the probability of two consecutive options were equal separately for the first switch latencies ($p(T_S) = .17$: $p(T_M) = .17$, $p(T_S) = .33$: $p(T_M) = .33$, and $p(T_S) = .415$: $p(T_M) = .415$) and the second switch latencies ($p(T_M) = .17$: $p(T_L) = .17$, $p(T_M) = .33$: $p(T_L) = .33$, and $p(T_M) = .415$: $p(T_L) = .415$). If participants made local probabilistic judgments between consecutive pairs, switch latencies would not be expected to differ across these equal probability conditions; however, if participants made global probabilistic judgments, a significant difference in switch latencies across these equal probability conditions would be observed. The pair-wise comparisons revealed that the first switch latencies did not differ across different equal-probability pairs, all ps > 0.30; whereas there was a significant difference in second switch latencies between $p(T_M) = .17$: $p(T_L) = .17$ and $p(T_M) = .415$: $p(T_L) = .415$ conditions (see results above).

Given the results of the first set of analyses of the switch latencies, it is possible that first switch latencies constrained the timing of the second switch latencies. To address this possibility, the relation between normalized first and second switch latencies of each participant was investigated by using linear regression. Next, the obtained slopes were compared to the value of 0. The one-sample t-tests revealed that the obtained coefficients were significantly higher than 0 in all experimental conditions, all ps < 0.001 (see Table 3).

The comparison of CV values for first switch latencies did not reveal any significant difference across conditions, $F(2, 18) = 0.79$, $p = 0.47$, $\eta_p^2 = .08$. Similarly, no significant difference emerged between CV values for the second switch latencies observed in different probability conditions, $F(2, 17) = 0.37$, $p = 0.69$, $\eta_p^2 = .04$. These results suggest that scalar property held for the timed responses of human participants.

Table 3. One-sample *t*-test comparisons of the linear regression slopes of second switch latencies on first switch latencies to the value of 0 separately for different probability conditions (human data)

| Probability condition	M_{beta}	SD_{beta}	$t(9)$
.17: .415: .415	.55	.10	18.39*
.17: .17: .66	.58	.10	18.07*
.33: .33: .33	.61	.08	22.79*
.415: .415: .17	.52	.13	13.01*
.66: .17: .17	.57	.10	17.10*

*Note: *$p < 0.001$

In order to examine whether participants tracked optimal switch latencies, each individual's mean empirical switch latencies observed in different probability conditions was regressed on the corresponding optimal switch latencies. The one-sample *t*-test comparison of obtained regression slopes ($M = 2.15$, $SD = 0.78$) to the value of 0 revealed a significant difference for first switch latencies, $t(9) = 8.68$, $p < 0.001$. However, the obtained regression slopes for second switch data ($M = -0.23$, $SD = 2.11$) were not significantly different from 0, $t(9) = -.34$, $p = 0.74$. These results indicate that, human participants tracked the optimal strategies in their first switches whereas this was not the case for their second switches.

In order to further investigate the possible deviations from optimal switch latencies, the empirical and optimal switch latencies in each probability condition were compared. Empirical first switch latencies in $p(T_S) = .66$: $p(T_M) = .17$ condition ($M = 2.72$, $SD = 0.15$) were significantly longer than optimal first switch latencies for this condition ($M = 2.59$, $SD = 0.08$), $t(9) = 4.22$, $p = 0.002$. There was also a significant difference between optimal ($M = 2.45$, $SD = 0.03$) and empirical ($M = 2.54$, $SD = 0.07$) first switch latencies in $p(T_S) = .415$: $p(T_M) = .415$ condition, $t(9) = 3.60$, $p = 0.006$ (Holm-Bonferroni corrected). There were no other significant differences. The analyses conducted for the second switch latencies revealed that the empirical switch latencies were significantly longer than the optimal switch latencies in all probability conditions, (all ps < 0.05, Holm-Bonferroni corrected).

f. Mouse data. In the long trials, the correct response pattern was first going to the short location, then switching from the short location to the medium location, and lastly switching from the medium location to the long location. In order to evaluate whether subjects consistently displayed this specific sequence, the proportion of the long trials in which mice exhibited switching behavior in an incorrect order was calculated (i.e., short-long, mid-short, long-mid, long-short). First this proportion for all long trials was calculated and it was observed that the subjects followed an incorrect sequence in 21, 11, and 16% of the long trials in the $p(T_S) = .2$, $p(T_S) = .33$, and $p(T_S) = .6$ conditions, respectively. However, in order to investigate this proportion observed in the trials where the subjects exhibited task-engagement and task-representative performance, the analysis was repeated using the trials where there was at least a first switch from the short to the medium location. This calculation revealed that the subjects followed an incorrect sequence in 4, 7, and 9% of the trials for increasing short trial probability conditions, respectively. These trials were not included in the analyses.

Next, in order to investigate whether mice could time three durations accurately, response rates (in 200 ms bins) of each response type (short, medium, long) were calculated separately for each subject. The normalized average response curves for each probability condition are shown in Figure 9. Visual inspection of this figure suggests that mice could accurately time the short interval but *underestimated* the medium interval as manifested in the longer peak location of the response curves compared to the target duration. This shift from the medium duration can be explained by the travel time (i.e., the time spent switching from the short to the medium location). Since mice were not tested in probe trials for the long target intervals, it is not possible to evaluate the accuracy for time judgments for the long target time.
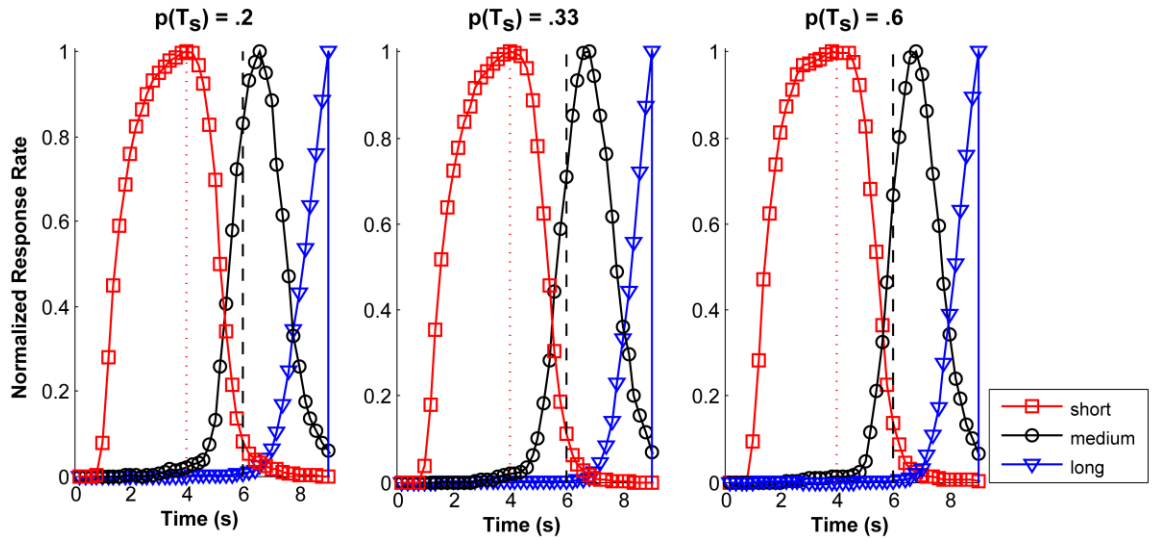
Figure 9. Average response curves (normalized by the maximum response rate for each response type) for short, medium, and long response types obtained from long trials in different probability conditions. Vertical lines correspond to the target latencies (dotted line: short latency, dashed line: medium latency, solid line: long latency).

The first and second target switch latencies were estimated from the Gaussian portion of the Exponential Gaussian mixture distribution function fits to subjects' data. Figure 10 depicts the average first and second switch latencies for different probability conditions. There was a significant increase in first switch latencies with increasing short trial probability, $F(2, 36) = 9.60$, $p < 0.001$, $\eta_p^2 = .35$. Follow-up pair-wise comparisons revealed a significant difference only between $p(T_S) = .2$ ($M = 4.97$, $SD = 0.04$) and $p(T_S) = .6$ ($M = 5.23$, $SD = 0.03$) conditions, $p = 0.003$ (Holm-Bonferroni corrected). There was a significant effect of probability condition on the second switch latencies as well, $F(1, 24) = 4.43$, $p = 0.03$, $\eta_p^2 = .21$. As pair-wise comparisons indicated, there was a significant difference in switch latencies between $p(T_L) = .6$ ($M = 7.18$, $SD = 0.33$) and $p(T_L) = .2$ ($M = 7.44$, $SD = 0.21$) conditions, $p = 0.001$ (Holm-Bonferroni corrected).
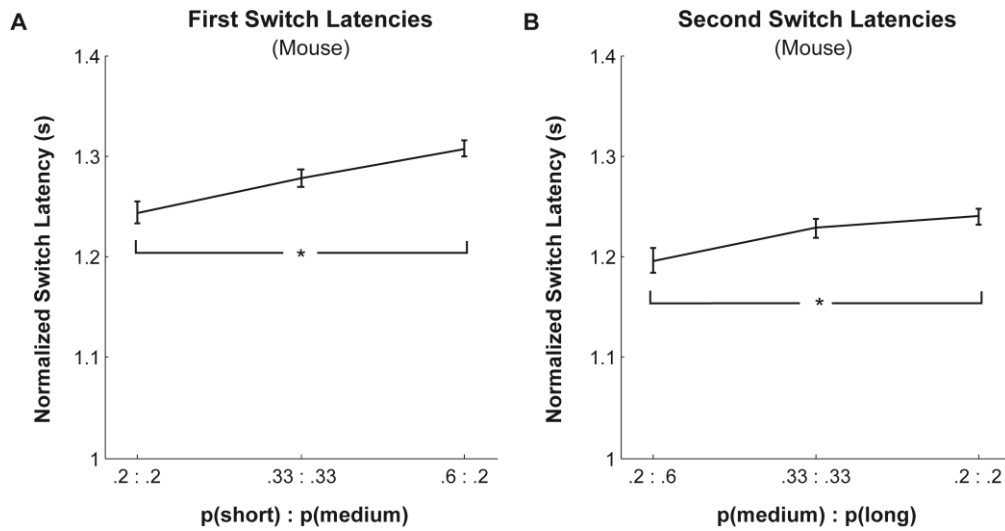
Figure 10. First (A) and second (B) mean switch latencies (normalized by 4 and 6 s, respectively) of mice for different probability conditions (*$p < 0.05$).

In order to investigate whether subjects made local or global judgments between neighboring options, the pair-wise comparisons were evaluated between those conditions where the probability of two consecutive options was equal separately for first switch latencies ($p(T_S) = .2$: $p(T_M) = .2$ and $p(T_S) = .33$: $p(T_M) = .33$) and second switch latencies ($p(T_M) = .2$: $p(T_L) = .2$ and $p(T_M) = .33$: $p(T_L) = .33$). For the first switch latencies, a marginally significant increase from $p(T_S) = .2 : p(T_M) = .2$ ($M = 4.97$, $SD = 0.04$) to $p(T_S) = .33 : p(T_M) = .33$ ($M = 5.11$, $SD = 0.03$) condition was observed, $p = 0.052$ (Holm-Bonferroni corrected). For the second switch latencies, the difference between equal-probability pairs did not approach significance, $p = 0.45$ (Holm-Bonferroni corrected).

The CV values for both first and second switch latencies were compared across different probability conditions. The results revealed no significant effect of stimulus probability condition on CV values obtained from the first switch latencies, $F(2, 36) = 1.02$, $p = 0.37$, $\eta_p^2 = .05$. Similarly, CV values obtained from the second switch latencies did not exhibit a significant change between different stimulus probability conditions, $F(2, 36) = 0.94$, $p = 0.40$, $\eta_p^2 = .05$. These results suggest that scalar property also held for the timed responses of mice.

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In order to investigate the possible relation between first and second switch latencies of mice, linear regression was conducted on an individual subject basis. The mean slopes were .56, .62, and .70 for increasing short trial probability conditions, respectively. The one-sample t-test comparisons of the obtained regression slopes to the value of 0 revealed a significant difference for all probability conditions ($p(T_S) = .2$: $t(18) = 9.17$; $p(T_S) = .33$: $t(18) = 26.96$; $p(T_S) = .6$: $t(18) = 16.10$; all ps < 0.001).

The mean differences between optimal and empirical switch latencies were also investigated separately for different probability conditions. The results indicated that subjects' empirical first switch latencies were significantly longer than the optimal in $p(T_S) = .33$ ($M_{emp} = 5.11$, $M_{opt} = 4.95$, $t(18) = 4.81$) and $p(Ts) = .6$ ($M_{emp} = 5.23$, $M_{opt} = 5.08$, $t(18) = 4.81$) conditions, $p < 0.001$ (Holm-Boferroni corrected). There was no significant difference between the optimal and empirical second switch latencies in any probability condition (all ps > 0.05).

3. Discussion

The second study investigated whether and how stimulus probabilities are incorporated into time-based decisions of humans and mice in scenarios that required them to make subsequent decisions within a given trial in a prospective decision-making task. In order to study this question, humans and mice were tested in a three alternative timed switch task. In this task, each of the three different delays-to-reward was associated with a different reward location. In a given trial, only one of the trial types and thus reward locations was armed without marking it with a discriminative stimulus. The probability of different trial types was manipulated across different experimental conditions. In trials where the long-latency-related location was active (i.e., long-latency trial was in effect), subjects were expected to switch first from the short location to the medium location if the reward was not

delivered after the short-latency, and they would switch to the long-latency-related location if the reward was not delivered after the medium-latency either. Consequently, they would make two subsequent time-based decisions in the long trials. The primary question was whether the switch latencies of humans and mice between short-medium options and medium-long options were sensitive to probabilistic manipulations. Furthermore, the specific design of this study aimed to investigate if the subjects were treating the probabilities within a pair locally or if the probabilities were treated globally.

The results of this study showed that both humans and mice exhibited the expected sequential timed switching behavior in the dual-switch task. Additionally, their first switches were sensitive to the probabilistic task contingencies such that subjects switched earlier if the medium trial had a higher probability whereas they switched later if the short trial probability was higher. Thus, subjects incorporated the stimulus probabilities into their decisions about when to leave the first option for the next one. On the other hand, the second switch latencies of humans did not show the same level of sensitivity to the probabilistic information as their first switch latencies. The analyses suggested a constraining effect of the first switch latencies on the second switch latencies; as the time spent waiting on the first option increased, so did the time spent waiting on the second option irrespective of the probability condition. In all conditions, the empirical second switch latencies of humans were significantly longer than the optimal latencies (note also the occasional deviations from optimality for the first switch latencies). Consequently, the findings suggested that the human participants failed to adopt a probability-adaptive strategy (at least locally) in their second timed decisions.

Similar findings in humans were obtained in a previous study (Wu et al., 2009), which investigated optimality in a sequential motor task. In that study, participants were required to allocate a fixed time between two sequential movements each of which entailed touching a target on the screen. In this task, the optimal stay duration at the first target before moving to

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the second changed depending on the ratio of their associated gains. Wu et al. (2009) found that human participants spent more time than optimal on the first target, even when the gain associated with the second target was five times larger. Consistent with these findings, in the current study, the number of options emerged as a significant factor regarding the optimality of timed decisions of humans (especially in comparison to prior work that pointed at optimal temporal risk assessment performance). Despite that there were significant relations between the first and second switch latencies of mice, in contrast to the human data, this relation did not preclude probability-dependent adaptive timed response patterns in subsequent choice behavior. Consistently, the empirical and optimal target second switch latencies of mice did not show any significant difference (note deviations from optimality for the first switch latencies).

Overall, the findings point at a suboptimal tendency in the temporal discrimination performance of humans in decision-scenarios that contain multiple temporal options. These tendencies were not present or as apparent in the mouse data. This inter-species difference in adaptive timed behavior can be partially due to the decision biases in the case of human participants (e.g., Trommershäuser et al., 2005). Alternatively, the fact that the probability conditions in the mouse experiment were not as varied as they were for the human experiment might have led to the observed differential findings between mice and humans. The differential level of training for humans and mice is another potential factor that might have contributed to these inter-species differences. Finally, it is possible that the significant differences between different probability conditions in second switch latencies of mice are simply due to the residual effects of the modulation of the first switch latencies based on initial probabilities. To this end, note the parallelism between the lines representing first and second switch latencies in Figure 10 coupled with the lack of differences compared to $p(T_S) = p(T_M) = p(T_L) = .33$ condition. Thus, future studies are needed to conduct a more

comprehensive cross-species comparison of performance in this task.

Finally, the results suggest that humans compute and treat probabilities locally between each two consecutive option in their initial temporal decisions (i.e., first switches), as there were no significant differences in the first latencies between conditions that constituted equal probabilities of neighboring options. Despite the fact that these equal-probability conditions did not differ significantly, the visual inspection of the mean switch latencies revealed a trend to switch later as the total probability of these two options increased and the probability of the third option decreased (see Figure 9). Even though this trend could possibly suggest a global probability judgment across three options during temporal decision-making between the first two options, the fact that the differences were not significant prevented to reach such a definite conclusion. Unlike the first switches, the second switch latencies of humans differed significantly between one out of three comparisons of conditions where the neighboring options had equal probabilities.

Together with the suboptimal tendency to wait longer at the medium option, this result reveals the constraining effect of the first switch latency and/or the probability of the first two temporal options on the subsequent timed switching behavior of human participants. This was not the case for the mouse data; there were no significant differences in either first or second switch latencies of mice between conditions that contained equal probability of neighboring options. These results suggest that unlike humans, mice treated probabilities locally both for their initial and subsequent timed decisions. However, again note that even though the difference between conditions where the neighboring options had equal probabilities did not reach significance, there was a trend for a delay in switch latencies from the short to the medium option as their probabilities increased (see Figure 10). Similar to what is observed in the human data, this trend could suggest a global judgment across three options instead of a local judgment between each two consecutive pair of options for the first

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switch latencies. Again, it is not possible to reach such a definite conclusion as the analyses failed to reveal a significant difference between these conditions.

Consistent with previous studies that have demonstrated the modulatory effect of probabilistic information on perceptual two-alternative forced choice tasks (e.g. Carpenter & Williams, 1995; Leite & Ratcliff, 2011; Mulder, Wagenmakers, Ratcliff, Boekel, & Forstmann, 2012), the results of the second study indicated both humans and mice can modulate their time-based responses (at least the initial decisions) based on experienced probabilities. Thus, both human and nonhuman animals have been shown to process and integrate probabilistic information into their decisions pertaining to different domains, which suggests possibly a common evolutionary basis for this ability. With the current study, the scope of these previous findings has been expanded by including more than two options in a temporal decision-making task. As the endogenous uncertainty guides the integration of probabilistic contingencies for reward maximization, understanding how animals treat probabilities becomes an important topic of investigation. The current study has addressed how probabilities are treated (i.e., globally across all options or locally between each pair) when the task necessitates making subsequent timed decisions. Future studies can investigate this topic including a wider range of probabilistic conditions to establish a better understanding of the processes that underlay probabilistic sequential temporal judgments.

General Discussion

Recent studies conducted with human and non-human animals have shown that subjects could adjust their temporal decisions to the probabilistic information (Balcı et al., 2009; Kheifets & Gallistel, 2012). The scope of these studies was extended by the experiments conducted in this thesis to include retrospective decision-making and multiple temporal options as potential limiting conditions on optimality. The series of experiments

conducted in this thesis specifically investigated the temporal discrimination performance of humans and mice in scenarios with different probabilistic contingencies and evaluated the results within the framework of Statistical Decision Theory (Maloney, 2002; Maloney & Zhang, 2010; Mamassian, Landy, & Maloney, 2002).

The exogenous probability was the primary factor that was manipulated across different experimental conditions and this was achieved by changing the relative frequencies of different trial types. For the first study, the payoff matrix was also manipulated between two experiments (with vs. without penalty). Importantly, in this study participants were asked to make judgments regarding the already experienced durations in a retrospective fashion. Results of the first study indicated that in majority of the conditions subjects could exhibit optimal time-based behavior by adapting their decisions to the probabilistic manipulations. In other words, these experiments revealed that the optimal performance, which has been demonstrated in prospective decisions could be also applied to the retrospective decisions.

For the second study, a third temporal option was introduced to the switch task, the prospective analogue of the temporal bisection task used in the first study. Consequently, the task utilized in the second study required subjects (humans and mice) to make two consecutive time-based judgments in a subgroup of trials. The results of this study showed that humans and mice adjusted their initial temporal judgments based on experienced probabilities of different options and in directions predicted by optimality. Although, a similar result was observed for the subsequent decisions of mice, humans exhibited suboptimal adjustments of their subsequent temporal judgments in response to probabilistic information regarding the corresponding temporal options. This study suggested that the number of temporal options might constitute a limiting condition for the optimal temporal risk assessment performance of humans but not animals.

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Overall, the results of the current experiments are consistent with the findings of the earlier work as they demonstrated that by taking into account of both their endogenous timing uncertainty levels and probabilistic task contingencies, subjects could adopt a nearly optimal strategy in their retrospective decisions in a two-option scenario (Study 1) and in their initial temporal decisions in a task with three options requiring consecutive decision-making (Study 2). On the other hand, different from the previous studies that reported nearly optimal temporal decision-making performance of humans and non-human animals using two reference temporal options (Balcı et al., 2009; Kheifets & Gallistel, 2012), humans failed to adaptively adjust their subsequent decisions in accordance with the probabilistic information. On the other hand, mice showed sensitivity to the probabilistic information for both their initial and subsequent decisions. One possible explanation for this sub-optimal tendency could be that humans might deviate from optimality when they were required to make sequential decisions (see also Wu et al., 2009).

Every experiment conducted here contained symmetrical payoff matrices. The limits of the optimal retrospective temporal decision making and/or temporal decision making with multiple options can be further investigated by testing humans and mice with asymmetrical payoff matrices. .The experimental probabilistic manipulations utilized in the Study 2 were varied more for the human experiment compared to the mouse experiment. Moreover, mice received more training compared to the human participants. The between species differences might indeed be due to these procedural differences. Further studies are needed to test more comparable experimental conditions across species to provide a better comparative understanding of the sequential temporal decision-making.

Conclusion

In conclusion, the findings stated here indicate that different probabilistic contingencies were incorporated into the temporal discrimination decisions of humans and mice. However, the number of temporal options constituted a limiting factor for the optimality of human time-based decision making. Consequently, these experiments extended the scope of temporal risk-assessment studies to include retrospective temporal decision-making and defined a limiting condition for human optimal time-based decisions.

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