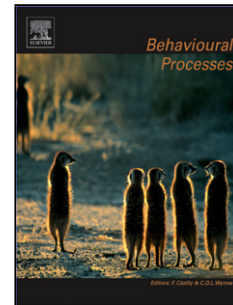# Accepted Manuscript

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Trial Frequency Effects in Human Temporal Bisection: Implications for Theories of Timing

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Abstract

To contrast the classic version of the Scalar Expectancy Theory (SET) with the Behavioral

Economic Model (BEM), we examined the effects of trial frequency on human temporal

judgments. Mathematical analysis showed that, in a temporal bisection task, SET predicts

that participants should show almost exclusive preference for the response associated with

the most frequent duration, whereas BEM predicts that, even though participants will be

biased, they will still display temporal control. Participants learned to emit one response

(R[S]) after a 1.0-s stimulus and another (R[L]) after a 1.5-s stimulus. Then the effects of

varying the frequencies of the 1.0-s and 1.5-s stimuli were assessed. Results were more

consistent with BEM than with SET. Overall, this research illustrates how the impact of non-

temporal factors on temporal discrimination may help us to contrast associative models such

as BEM with cognitive models such as SET. Deciding between these two classes of models

has important implications regarding the relations between associative learning and timing.

Keywords: interval timing, cognitive decision rules, associative decision rules, scalar

expectancy theory, behavioral economic model, trial frequency, temporal bisection

Trial Frequency Effects in Human Temporal Bisection: Implications for Theories of Timing

1. Introduction

Associative learning is the ability of living organisms to perceive contingency relations between two events. Interval timing is the ability of living organisms to perceive temporal intervals between two events. In recent years, several researchers have proposed that those two abilities are closely linked and perhaps arise from a common mechanism. On one hand, some researchers (i.e. Balsam, Drew, & Gallistel, 2010; Balsam & Gallistel, 2009; Gallistel & Gibbon, 2009) have proposed that interval timing underlies associative learning. These researchers usually rely on the scalar expectancy theory (SET; Gibbon, Church, & Meck, 1984) of interval timing, according to which animals encode representations of temporal intervals by way of a pacemaker-accumulator mechanism, which representations are then stored in long-term memory. On the other hand, some other researchers have viewed the problem the other way round and proposed that associative learning underlies interval timing. This is, for instance, the case in Machado's Learning-to-Time model (LeT) model (Machado, 1997; Machado, Malheiro, & Erlhagen, 2009) and Jozefowiez, Staddon, and Cerutti's (2009) Behavioral Economic Model (BEM), in which the learning of associations between internal, time-dependent states and responding results in interval timing (see also Ludvig, Sutton, & Kehoe, 2012). Those associations are supposed to follow the general principles of conditioning that are embedded in classical models of learning such as the Bush-Mosteller integrator (Bush & Mosteller, 1955; Stout & Miller, 2007) or the Rescorla-Wagner model (Rescorla & Wagner, 1972). Overall, those theories are representative of what Balsam et al. (2010) called a "componential trace" model of learning wherein "the nominal (conditioned stimulus) is actually composed of multiple successive cues that can independently acquire associations with the (unconditioned stimulus)" (Balsam et al., 2010, p. 6; see Buhusi &

Schmajuk, 1999; Grossberg & Schmajuk, 1989; Vogel, Brandon, & Wagner, 2003, for similar approaches but using different learning rules).

Hence, the debate over the relationship between timing and associative learning is tied to the debate over alternative accounts of interval timing. In this article, we will try to contribute to the former by pitting the predictions of two competing models of timing, SET and BEM, which stand on opposing sides of the debate. For this, we tested their predictions in what is arguably the most well studied timing procedure: the bisection task (Allan & Gibbon, 1991; Church & Deluty, 1977; Stubbs, 1968; Wearden, 1991).

In a bisection task, the participant is presented with two stimulus durations, short (S) and long (L), and is reinforced for emitting response R(S) following S and response R(L) following L. In most bisection studies, the participant is then tested on nonreinforced probe trials in which the stimulus duration varies between S and L. Results show that the probability of emitting R(L) during the test trials increases with the stimulus duration. The so-called bisection point is the duration T for which the participant is indifferent between R(S) and R(L).

According to BEM, the beginning of a trial initiates a sequence of time-dependent states. Each state is specifically tuned to a stimulus duration and the probability of that state becoming active increases as the current stimulus duration gets closer to the stimulus duration of that state. Only one state is active at a time. If R(S) (or R[L]) is emitted while the subject is in state x, the association between state x and R(S) (or R[L]) changes according to a linear operator rule (e.g., Bush & Mosteller, 1955), increasing in the case of reinforcement and decreasing in the case of nonreinforcement. Moreover, BEM assumes a logarithmic encoding of time: The active state at interval t, x(t), is a random variable drawn from a Gaussian distribution with mean $ln\ t$ and standard deviation k (see Jozefowiez et al., 2009, in press, for arguments justifying the choice of a log representation over a linear representation; see also

Dehaene, 2001; Roberts, 2008 and Yi, 2008 for theoretical and empirical arguments favoring a log over a linear representation). We call the random variable x the short-term memory (STM) representation of an interval *t*. In addition, let *V1(x)* be the strength of the association between *x* and R(S) and *V2(x)* be the strength of the association between *x* and R(L). Then, whenever the subject is in state x at the end of an interval, R(L) is emitted if

$$V1(x) < bV2(x) \qquad (1)$$

where *b* is a free parameter representing all sources of bias other than the reinforcement probabilities or the trial frequencies, such as any unconditioned preference for one response over the other. Under these assumptions, it can be shown (see the Appendix) that *r(t)*, the probability of emitting R(L) after a stimulus of duration *t*, is equal to

$$r(t) = \Phi\left[\frac{\ln t - \ln\left(\beta^{\frac{k^2}{\ln\frac{L}{S}}} \sqrt{SL} \right)}{k} \right] \qquad (2)$$

with

$$\beta = \frac{1}{b} \frac{F(S)}{F(L)} \frac{P(S)}{P(L)} \qquad (3)$$

F(S) is the frequency of trials on which the stimulus lasts S units of time, *P(S)* is the probability of reinforcement given a correct response on such a trial, *F(L)* and *P(L)* represent the equivalent quantities for trials on which the stimulus lasts L units of time, and Φ is the standard Gaussian distribution function. The bisection point is the value of *t* for which equation (2) is equal to 0.50, which implies $t = \beta^{\frac{k^2}{\ln\frac{L}{S}}} \sqrt{SL}$. Figure 1 shows how it varies according to the bias *ß* in a 1.0-s vs. 1.5-s bisection procedure (*k* was set to 0.2, which is the typical value this parameter takes when we fitted bisection data with BEM).

The foregoing predictions cannot be directly contrasted with SET's corresponding predictions because there are multiple versions of SET, differing among themselves in details such as the decision rule or the rules to store the temporal representations. In fact, SET is more accurately conceived of as a framework for building models than a model itself. Hence, to test the theory empirically and compare it with other models, one needs to choose one of SET's specific instances. In this article, we focus on the classical SET model that Gibbon (1981) used to account for the bisection procedure. We will come back in the General Discussion to the implications of our data for other versions of SET.

Let us assume a bisection trial lasting *t* s. According to SET, at stimulus onset a pacemaker starts emitting pulses at a rate of *a* pulses per second. Those pulses accumulate in STM. After *t* s, the average number of pulses accumulated in STM is $a{\times}t$. The number of pulses associated with the reinforcement of R(S) (*aS* on the average*)* and R(L) (*aL* on the average) are stored in long-term memory (LTM). The decision to respond is based on a comparison between the STM representation (*at*) with the two LTM representations (*aS, aL)* according to a ratio rule. Specifically, according to SET, the subject chooses R(L) whenever

$$\frac{at}{aS} > \beta\frac{aL}{at} \tag{4}$$

where *ß* is a free-parameter representing response bias. Following Gibbon (1981), we assumed that the LTM representations are noiseless while the STM representation is a random variable. Under these assumptions, it can be shown (see the Appendix) that the probability of choosing R(L) given a t-sec stimulus equals

$$r(t) = \Phi\left(\frac{t - \sqrt{\beta SL}}{kt}\right) \tag{5}$$

with a bisection point at $\sqrt{\beta SL}$. It is through variation of *ß* that SET can account for reinforcement-induced biases or trial-frequency induced biases (Wearden & Gringrod, 2003). Hence, one needs to know how to relate *ß* to *F(S), P(S), F(L),* and *P(L)*. Gibbon (1981)

suggested decomposing β into two components, one corresponding to a side preference for one response, the other to "the payoff differential familiar from signal detection theory" (Gibbon, 1981, p. 65), that is to say P(S)/P(L) (Wickens, 2002). Hence, we used equation (3), which not only satisfies Gibbon's suggestion concerning the payoff differential, P(S) and P(L), but extends naturally to different stimulus frequencies, F(S) and F(L).

Figure 1 shows how the bisection point varies with β in a 1.0-s vs. 1.5-s bisection procedure according to Equation (5). The contrast with the predictions from BEM is striking. Compared to BEM, SET is more sensitive to bias: The bisection point goes below or above the reference durations to such an extent that, if we restrict the testing range to values between those two durations (as in most studies with the bisection procedure), we will observe exclusive preference for the more frequent/reinforced response. This is a direct consequence of the combination of a linear representation with scalar variance with a ratio decision rule. By contrast, according to BEM, even when performance is biased toward the more frequent/reinforced side, the bisection point should remain clearly between the two reference durations. To summarize, BEM predicts that, if trial frequency (or reinforcement) is manipulated in a bisection task, one should still see good temporal control, even though the performance will be biased toward the more frequent/reinforced response. On the other hand, except in the case of a very small frequency/reinforcement manipulation, SET predicts exclusive preference for the more frequent/reinforced response.

We tested this clear-cut prediction in the present study. We decided to manipulate trial frequency instead of the probability of reinforcement because this latter variable is partly under the control of the participant. This fact could lead to critical discrepancies between the scheduled and the obtained reinforcement probabilities. As a result, quantitative fits to the data by BEM and SET would be difficult. In contrast, trial frequency is independent of the participant's behavior.

Human participants were exposed to a 1.0-s vs. 1.5-s bisection task. This fairly difficult discrimination was used intentionally because Equation (2) makes clear that no bias effect is predicted by BEM if the discrimination is too easy. Participants were trained to emit R(S) after a 1.0-s stimulus and R(L) after a 1.5-s stimulus. In the experimental conditions, one type of trial was three times more frequent than the other, whereas in the control condition the two types of trials had the same frequency. The two experimental conditions correspond to trial frequency ratios at the extremes of the x-axis in Figure 1. The participants were then tested on probe trials with durations ranging from 1.0 to 1.5 s. SET predicts good temporal control in the control condition but exclusive preference for the response associated with the more frequent duration in the experimental conditions. In contrast, BEM predicts temporal control in all conditions, although performance will be biased toward the response associated with the more frequent duration in the experimental conditions.

2. Materials and method

2.1. Participants and Apparatus

One hundred and twenty-three undergraduate students at SUNY-Binghamton participated in the experiment to meet a course requirement. Participants were randomly assigned to one of three groups: Bias-Short ($n = 44$), Bias-Long ($n = 41$), and Control ($n = 38$). They had no previous experience with temporal discrimination tasks. All testing was done on six IBM compatible PCs. Inputs were made through a standard computer keyboard. All testing visuals were displayed on 14-inch VGA monitor screens. E-prime was the software application used as the testing program.

2.2. Procedure

2.2.1 Training. There were two phases, training and testing. During the training phase, participants sat in front of the computer and then read the following instructions displayed on the computer screen:

"Thank you for participating in our study of time perception.

You will see a red circle appearing in the middle of the screen that will come on for a time. Once the circle disappears, you will be asked to choose between pressing number 1 or number 2 on the keyboard. Based on the duration of the circle, you will have to figure out which number is correct. Once you have made your choice, a screen will appear telling you if you were correct or not and stating your percent of correct answers across all trials so far. Your goal is to keep this percentage as high as possible.

IMPORTANT: Please do not count or perform rhythmic activities during the experiment. Please press the space bar when you are ready to begin."

Instructions to avoid counting or performing rhythmic activities have been found to be successful in reducing biases that may be produced by adopting a chronometric counting strategy (Grondin, Ouellet, & Roussel, 2004).

Each trial began with the sample stimulus, a red circle, 10 cm in diameter, displayed in the center of the screen for either 1.0 or 1.5 s. At the end of the stimulus, the sample disappeared and the participant was prompted to choose between pressing number 1 or number 2 on the keyboard. Once the participant responded, a feedback screen was presented for 2 s, informing the participant whether the response was correct as well as the percentage of correct responses up to that trial. If the response was correct, participants were shown the screen message "Correct response!" in blue bold letters. Just below that, the following message was displayed in black letters: "Percentage of correct responses so far x %". If the response was incorrect, participants were shown the screen message "Incorrect response!" in bold red letters with the message, "Percentage of correct responses so far x %" displayed in black letters just below. For half of the participants in each of the three experimental groups,

choosing number 1 after the 1.0-s stimulus and choosing number 2 after the 1.5-s stimulus was reinforced. For the other half of the participants, these contingencies were reversed.

All groups were exposed to 60 trials, but the proportion of 1.0-s and 1.5-s trials differed across groups: in the Control group, the participants were exposed to 30 1.0-s trials and 30 1.5-s trials; in the Bias-Short group, the participants were exposed to 40 1.0-s trials and 20 1.5-s trials; and in the Bias-Long group, the participants were exposed to 20 1.0-s trials and 40 1.5-s trials. The order of presentation of trials for each participant was determined randomly.

2.2.2 Testing. Immediately after training was completed, participants read the following instructions:

"Now we are going to continue, but you will not be given feedback.

Your percentage of correct answers will still be computed but will not appear on the screen.

IMPORTANT: Please do not count or perform rhythmic activities during the experiment.

Please press the space bar when you are ready to continue."

Testing consisted of four cycles of six trials each. The test trials were identical to the training trials except that, in addition to 1.0-s and 1.5-s stimuli, 4 new stimulus durations (1.1, 1.2, 1.3, and 1.4 s) were presented and no feedback was given to the participant. Instead, after each response the participants were presented with a blank screen for 2.0 seconds. The order of presentation of the stimuli during each cycle was determined randomly for each participant. Once the test phase was over, a screen thanking and debriefing the participants was displayed.

3. Results

Individual psychometric functions were fitted with a cumulative probability Gaussian function using the nonlinear least-square Marquardt-Levenberg algorithm (Levenberg, 1944). For each participant, the mean of the Gaussian function estimated the bisection point and the standard deviation of the Gaussian function estimated sensitivity to time.

According to BEM, estimates of the bisection point should fall between 1.0 s and 1.5 s for all groups, whereas according to SET this should happen only for the control group. According to SET, because participants should show exclusive preference toward the more frequent (i.e., reinforced) response, the estimates of the bisection point should fall below 1.0 s for the Bias-Short group and above 1.5 s for the Bias-Long group.

3.1. Participants displaying exclusive preference

Only a small percentage of participants had bisection points outside the testing range: 7 (out of 38) in the Control group, 14 (out of 41) in the Bias-Long group and 12 (out of 44) in the Bias-Short group. Given that these subjects showed no modulation of performance as a function of the stimulus duration (i.e., they exhibited exclusive preference for one side or the other), the estimated bisection points were often extremely large or small, making their absolute values meaningless; hence, we do not report these values here. However, the average proportion of these participants responding on R(L) (the response associated with the 1.5-s stimulus) is meaningful, as it allows us to determine whether the participants in the various groups who had bisection points outside the testing range were biased towards different responses. According to SET, the proportion of these participants responding on R(L) should have been higher in the Bias-Long group than in the Control group and lower in the Bias-Short group than in the Control group. Figure 2 shows the mean proportion of responding on R(L) as a function of group for participants with bisection points outside the testing range. As can be seen, all groups displayed a slight bias against R(L). However, and contrary to SET, the proportion of responding on R(L) in the Bias-Long group was not higher

than the proportion of responding on R(L) in the Bias-Short group. An ANOVA on the

proportion of responding on R(L) using group (Bias-Short, Control, Bias-Long) as a factor

failed to find any significant effect, $p > .05$. These participants probably failed to pay

attention to the temporal dimension of the task. The number of participants in the Control

group with bisection points outside the testing range gives us an estimate of the number of

participants not paying attention to the temporal dimension of the task (note that all models

predict temporal control in the Control condition). Though it might seem that this number

was a bit lower than in the experimental groups, there was no significant relationship between

group and the proportion of participants showing temporal control, $\chi^2(2) = 2.49, p > .05$.

3.2. Participants showing temporal control

The remaining participants (31 of 38 in the Control group, 27 of 41 in the Bias-Long group,

and 32 of 44 in the Bias-Short group) had their bisection point within the test range. The

analysis below is restricted to these participants. According to BEM, the bisection point in

the Bias-Short group should be higher than the bisection point in the Control group, and the

bisection point in the Bias-Long group should be lower than the bisection point in the Control

group. To see if this is the case, Figure 3 shows the mean bisection points and sensitivities to

time as a function of group. Most human studies report a bisection point at the arithmetic

mean of the two trained durations, (e.g. Allan, 2002b; Allan & Gerhardt, 2001; Brown,

McCormack, Smith, & Stewart, 2005; Droit-Volet & Wearden, 2001; Wearden, 1991;

Wearden & Ferrara, 1995, 1996), whereas it is usually at the geometric mean in nonhuman

animal studies (Church & Deluty, 1977; Stubbs, 1968), a result also reported in a few human

studies (e.g., Allan & Gibbon, 1991; Provasi, Rattat, & Droit-Volet, 2011). In our study, the

difference between the arithmetic and the geometric mean is very small (1.25 s vs. 1.22 s).

Hence, even though the mean bisection point in the control group is closer to the arithmetic

than the geometric mean, the variation around the mean is large enough to preclude any

conclusion regarding whether the participants bisected the interval at the arithmetic or geometric mean. Still, as predicted by BEM, the bisection point shifted to the right in the Bias-Short group and to the left in the Bias-Long group.

With respect to sensitivity to time, the bottom panel of Figure 3 shows that the two experimental groups were slightly more sensitive than the Control group (lower standard deviations), but the mean effect is accompanied by significant variation within each group. The same conclusion can be drawn from the psychometric curves showing the proportion of responding on R(L) as a function of stimulus duration (see Figure 4). Because we used a pair of sample durations that is harder to discriminate than the pairs used in previous studies (e.g. Allan, 2002b; Allan & Gerhardt, 2001; Brown, McCormack, Smith, & Stewart, 2005; Droit-Volet & Wearden, 2001; Wearden, 1991; Wearden & Ferrara, 1995, 1996), we obtained a psychometric curve for the Control group slightly flatter than in those studies. Still, responding in the Bias-Short group was biased toward R(S) (the response associated with 1.0-s stimulus) relative to the control group and, similarly, responding in the Bias-Long group was biased toward R(L) (the response associated with the 1.5-s stimulus relative to the control group.

Statistical analysis confirmed those impressions. An analysis of variance (ANOVA) on the bisection point using group (Control, Bias-Long, Bias-Short) as a factor yielded a significant effect, $F(2, 86) = 13.75$, $MSE = .01$, $p < .01$. Planned comparisons using Fisher's LSD test revealed a difference between the Bias-Short and the Bias-Long group, $p < .01$, the Bias-Long and the Control group, $p < .05$, and the Bias-Short and the Control group, $p < 01$. In the same way, a repeated measure ANOVA on the proportion of responding on R(L) using stimulus duration and group as factors found a main effect of stimulus duration, $F(5, 430) = 169.4$, $MSE = .04$, $p < .01$, and of condition, $F(2, 86) = 11.92$, $MSE = .09$, $p < .01$. Planned comparisons with the LSD test found significant difference between the Bias-Short group and

both the Bias-Long group, $p < .01$, and the Control group, $p < .05$ as well as between the

Bias-Long and the Control group, $p < .05$. An ANOVA on the sensitivity to time using group

as a factor failed to find any significant effect, $p > .05$.

4. Discussion

The data were not consistent with SET's predictions. Only a minority of participants had a

bisection point outside of the testing range, and those participants did not display the pattern

predicted by SET in that they showed an unconditional preference for the response associated

with the 1.0-s stimulus. SET predicted this pattern only for the Bias-Short group; the Bias-

Long group should have been biased toward the response associated with the 1.5-s stimulus.

By contrast, the data from the participants whose bisection points fell within the testing range

were consistent with BEM. Compared to the Control group, participants in the Bias-Short

group were biased toward the response associated with the 1.0-s stimulus, whereas

participants in the Bias-Long group were biased toward the response associated with the 1.5-s

stimulus.

The foregoing conclusions are based on qualitative differences. The fact that trial

frequency was not affected by the participants' behavior allows us to quantitatively fit the

model to the data. The bottom panel of Figure 5 shows how BEM fitted the data. To obtain

those figures, Equation (2) was fitted to the Control group using the nonlinear least-squares

Marquardt-Levenberg algorithm (Levenberg, 1944). The two free parameters of the model, b

and k, were then frozen. The $F(S)/F(L)$ ratio was then varied to simulate the trial frequency

manipulation. As can be seen, BEM accurately estimates the magnitude of the effect of trial

frequency on performance.

The top panel of Figure 5 shows the predictions made by SET, computed using the

same method as for BEM: Equation (5) was fitted to the data from the Control group using

the Marquardt-Levenberg algorithm; the two free parameters of the model (b and $k)$ were

then frozen while the *F(S)/F(L)* ratio varied to simulate the trial frequency manipulation. Consistent with Figure 1, the bottom panel of Figure 5 shows that SET overestimates the effect of the trial frequency manipulation, predicting almost exclusive preference for the response associated with the most frequent stimulus duration in the experimental groups.

5. Conclusions

In this study, we biased performance in a temporal bisection task by manipulating trial frequency. Even though most participants still displayed temporal control, their performance was biased toward the response associated with the more frequent stimulus duration. Timing models diverge regarding the size of the predicted bias effect. SET predicts that even a small difference in trial frequencies should lead to an almost exclusive preference for the side associated with the higher stimulus frequency. By contrast, BEM predicts that the effect should be much weaker. In this regard, the data are more consistent with BEM, which also provided a reasonably accurate fit for the data.

Other models, such as Machado's Learning-to-Time model (Machado, 1997; Machado, Pinheiro, & Erlhagen, 2009), use the same associative structure as BEM, whereby performance is a function of associations between time-dependent states and responses. It is very likely that at least some of these associative models would have made the same qualitative and quantitative predictions as BEM. For example, simulations of the LeT model (Machado, 1997; Machado et al., 2009) led to a quantitative fit undistinguishable from that of BEM. Hence, the present data support not only BEM but a whole class of associative models of timing of which BEM is a prototypical instance (Jozefowiez & Machado, 2013).

Trial frequency and reinforcement effects are well documented in categorical perception tasks (see Maddox, 2002, for a review). A prior attempt to bias performance in a bisection task using rats as subjects failed to observe any effect of reinforcement magnitude on the location of the bisection point (Galtress & Kirkpatrick, 2010). In that study, rats

learned to discriminate 2-s and 8-s samples. Across conditions, correct responses were reinforced with different numbers of food pellets. Results showed no consistent biasing effect. Several reasons may explain why our results differ from the results obtained by Galtress and Kirkpatrick (2010). Of course, they worked with rats while we worked with humans, but we doubt that the difference in species is all that matters. The more likely explanation lies in Equation (2), which shows that BEM predicts that the size of a reinforcement-induced bias is a function of the difficulty of the temporal discrimination: The easier the discrimination, the smaller the magnitude of the bias effect. It seems reasonable to conclude that the discrimination in our study (1.0-s vs. 1.5-s) was significantly harder than the discrimination in their study (2-s vs. 8-s). In this case, the data would be inconsistent with SET, which predicts exclusive preference for the most reinforced response, no matter the difficulty of the discrimination (see Equation 3).

On the other hand, our results are consistent with those of Wearden and Grindrod (2003), who found reward magnitude effect in a human temporal generalization task and with those of Bizo and White (1994, 1995), who used a variant of the bisection procedure (the free-operant psychophysical procedure, FOPP) in pigeons. In that task, pigeons were given choice between two response keys. Key 1 was reinforced according to a variable-interval (VI) schedule but only during the first 25 s of a 50-s trial. Key 2 was reinforced according to a VI schedule but only during the last 25 s of the trial. When key 1 was reinforced at a higher rate than key 2, the pigeons switched to key 2 later in the interval than when the two keys provided the same reinforcement rate. Conversely, when key 1 was reinforced at a lower rate than key 2, the pigeons switched to key 2 earlier in the interval than when the two keys provided the same reinforcement rate (see also Guilhardi, MacInnis, Church, & Machado, 2007; Machado & Guilhardi, 2000; Stubbs, 1980). The bias effect observed by Bizo and White in the FOPP are very similar to the ones observed in the present study. Because of the

use of VI schedules, it is difficult to apply SET to the FOPP and to get quantitative predictions out of it. The same is true of a previous study by Stubbs (1976) which showed reinforcement-induced bias effect in a pseudo-bisection procedure. However, both BEM and LeT provide good quantitative accounts of the FOPP data (Jozefowiez et al., 2009; Machado & Guilhardi, 2000; Machado et al., 2009).

As stated in the introduction, SET is more a class of models than a single model. If the version of SET we tested failed to account for our findings, other versions might fare differently. For instance, to derive Equation (5), we followed Gibbon (1981)'s suggestion to ignore the noise in the long-term reference memories for the short- and long-duration samples (see Appendix). Otherwise, the equation for the probability to emit R(L) does not have an analytical form and cumbersome numerical simulations have to be used to obtain the psychometric function. Maybe that version of the model would fare better with the present data. But both Allan (2002a) and Rodríguez-Gironés and Kacelnik (2001) have claimed that empirical data support Gibbon (1981)'s hypothesis that noise in reference memory can be ignored when accounting for human temporal bisection performance. Hence, another solution would be to follow Wearden (1991) who substituted a difference decision rule for the ratio decision rule of the canonical SET model, thereby accounting for the fact that in humans the bisection point is often closer to the arithmetic mean than to the geometric mean. We verified that the over-sensitivity to trial frequency and reinforcement manipulation is greatly reduced in such a version of SET, which actually fits the data quite well. It predicts a slightly larger bias effect in the Bias-Long group than the one observed and as such provides a slightly worse fit to the data than BEM, but we need to have a better assessment of the reliability of the effect size that we observed in our data before concluding whether this is sufficient evidence to reject the modified SET version (details of the analysis for this version of SET are available in the supplementary materials).

Yet, even though SET can be salvaged thanks to its inherent polymorphism, its explanation remains a bit ad hoc when compared to BEM. In BEM, trial frequency and reinforcement probability bias performance because of core assumptions regarding the psychological process at hand. In SET, they influence performance just because we assumed so in Equation (3). Although this is a reasonable assumption, it is not derived from a more fundamental hypothesis regarding the psychological processes underlying behavior. Until Equation (3) is derived from more fundamental psychological principles, associative models like BEM will still provide the more satisfactory account of bias effects such as the ones demonstrated in the present experiments.

Finally, one could argue that the decisional bias demonstrated in this study has nothing to do with timing. Indeed, whether it is SET or BEM, the mapping between objective and subjective time and the variance in the representation is unaffected by reinforcement and trial frequency. What is affected is the mapping between the time representations and responding. Is it a timing effect, then? If by that we mean "does it affect the way the participant perceive duration?", there is no way for us to know and in the end, it does not matter. The point is that, depending on assumptions made concerning the representation of time and the nature of the decision mechanism, the effect of trial frequency/reinforcement probabilities will be different. Or to put it in another way, it does not matter if the bias effect is classified as a timing effect or not because, in the end, it does tell us something about timing: How time is encoded (linearly, logarithmically) and how it is represented (through associations or representations).

In conclusion, the present data add to the growing body of evidence concerning the role of non-temporal variables in timing. Even though they are more compatible with associative models, they call for further research into the way these variables affect interval timing. We believe that this is a critical development, as this study clearly illustrates that this

might provide a new path to discriminate between competitive accounts of time perception,

Notably, it provides a new means of approaching issues critical to theories of timing such as

whether subjective time is encoded logarithmically or linearly, and whether temporal

intervals are represented in long-term memory through associations or representations (see

Jozefowiez & Machado, 2013, for further discussions). This last question is at the core of the

current controversy regarding the relation between associative learning and timing. As stated

in the introduction, the view that temporal intervals are stored in long-term memory through

representations is necessary for approaches such as Balsam & Gallistel's (2009), which

reduce associative learning to timing. In contrast, the view that temporal intervals are stored

in long-term memory through associations is essential to theories adopting a "componential

trace" view of learning (e.g. Grossberg & Schmajuk, 1989; Jozefowiez et al, 2009; Ludvig, et

al., 2012; Machado, 1997; Machado, et al, 2009; Vogel et al., 2003), which theories reduce

interval timing to associative learning.

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Appendix

Accounting for bias effect in the temporal bisection with SET

Assume a t-sec long bisection trial. According to SET (Gibbon, 1981), a pacemaker starts emitting pulses at an average rate of *a* pulses per second. Those pulses accumulate in STM. After t sec, the number of pulses accumulated in STM is *x(t)*. Because the pacemaker rate varies across trials, *x(t)* is a Gaussian random variable with mean *at* and standard deviation *kat*. The participant also has LTM representations of the number of pulses associated with the reinforcement of R(S) (*x(S)*) and R(L) (*x(L)*). *x(S)* is a Gaussian random variable with mean *aS* and standard deviation *kaS,* and *x(L)* is a Gaussian random variable with mean *aL* and standard deviation *kaL*. To decide how to respond, the subject compares its STM representation, *x(t),* with his two LTM representations, *x(S)* and *x(L)* according to a ratio rule (Gibbon, 1981). R(L) is emitted if

$$\frac{x(t)}{x(S)} > \beta \frac{x(L)}{x(t)} \tag{A.1}$$

ß is a free-parameter representing response bias. Rearranging leads to

$$x(t) > \sqrt{\beta x(S) x(L)} \tag{A.2}$$

Following Gibbon (1981), we assume that the LTM representations are noiseless, that is, *x(S)=aS* and *x(L)=aL*. In this case, Equation (A.2) becomes

$$x(t) > a\sqrt{\beta SL} \tag{A.3}$$

The left-hand side of Equation (A.3) follows a Gaussian distribution with mean *at* and standard deviation *kat*. Hence, *r(t),* the probability of emitting R(L) following a sample *t*-s long is

$$r(t) = \Phi\left(\frac{t - \sqrt{\beta SL}}{kt}\right) \tag{A.4}$$

where Φ is the standard normal distribution. This corresponds to Equation (5) in the text.

Accounting for bias effect in the temporal bisection with BEM

Consider a bisection trial lasting t sec. BEM assumes that the STM representation of time t is a random variable x drawn from a Gaussian distribution with mean $ln\ (t)$ and standard deviation k. Let $V1(x)$ be the strength of the association between x and R(S), and $V2(x)$ be the strength of the association between x and R(L). R(L) is emitted if

$$V1(x) < bV2(x)$$ (A.5)

where b is a free-parameter representing all sources of bias other than the reinforcement probabilities or the trial frequencies, such as any unconditioned preference for one response over the other.

If R(S) (or R[L]) is emitted, $V1(x)$ (or $V2(x)$) is updated according to the Bush-Mosteller (1955) learning rule: It increases in the case of reinforcement and decreases otherwise. Hence, at the steady state, $V1(x)$ approximates the payoff for emitting R(S) when the time representation is equal to x, while $V2(x)$ approximates the payoff for emitting R(L) when the time representation is equal to x. Equation (10) can then be rewritten

$$F(S)P(S \mid x)P(S) < bF(L)P(L \mid x)P(L)$$ (A.6)

$F(S)$ is the frequency of a S-trial, whereas $P(S)$ is the probability of reinforcement for a correct response on an S-trial. $F(L)$ and $P(L)$ represent the equivalent quantities for L-trials. Let $G(x,m,d)$ be the density function of a Gaussian distribution with mean m and standard deviation d. Using Bayes' theorem and substituting $G[x,ln\ S,k]$ for $P(x|S)$ and $G[x,ln\ L,k]$ for $P(x|L)$ (see Jozefowiez et al., 2009, for the justification of this), Equation (11) can be rewritten

$$F(S)G[x,\ln S,k]P(S) < bF(L)G[x,\ln L,k]P(L)$$ (A.7)

Through tedious but straightforward manipulations, Equation (A.7) can then be rearranged in the following way

$$x > \ln\left(\beta^{\frac{k^2}{\ln\frac{L}{S}}}\sqrt{SL}\right)$$ (A.8)

with $\beta = \left(\dfrac{1}{b} \dfrac{F(S)}{F(L)} \dfrac{P(S)}{P(L)} \right)$. Because the right-hand term of Equation (A.8) is constant and the

left-hand term is a Gaussian random variable with mean ln t and standard deviation k, we

have

$$r(t) = \Phi \left[\frac{\ln t - \ln \left(\beta^{\frac{k^2}{\ln \frac{L}{S}}} \sqrt{SL} \right)}{k} \right] \qquad (A.9)$$

This corresponds to Equation (2) in the text.

Figure Captions

Figure 1. Bisection point as a function of bias in a 1.0-s vs. 1.5-s bisection task according to the SET and BEM. The horizontal line represents the geometric mean between 1.0 and 1.5 s.

Figure 2. Proportion of responding on R(L) (response associated with a 1.5-s stimulus) as a function of conditions for the participants whose bisection point fell below 1.0 s and above 1.5 s. Bars are standard errors.

Figure 3. Top panel: Mean bisection points as a function of conditions for the participants whose bisection point fell between 1.0 and 1.5 s. Bars are standard errors. Bottom panel: Mean sensitivity to time as a function of conditions for the participants whose bisection points fell between 1.0 and 1.5 s. Bars are standard errors.

Figure 4. Proportion of responding on R(L) (response associated with a 1.5-s stimulus) as a function of the test stimulus duration and conditions for the participants whose bisection point fell between 1.0 and 1.5 s. Bars are standard errors.
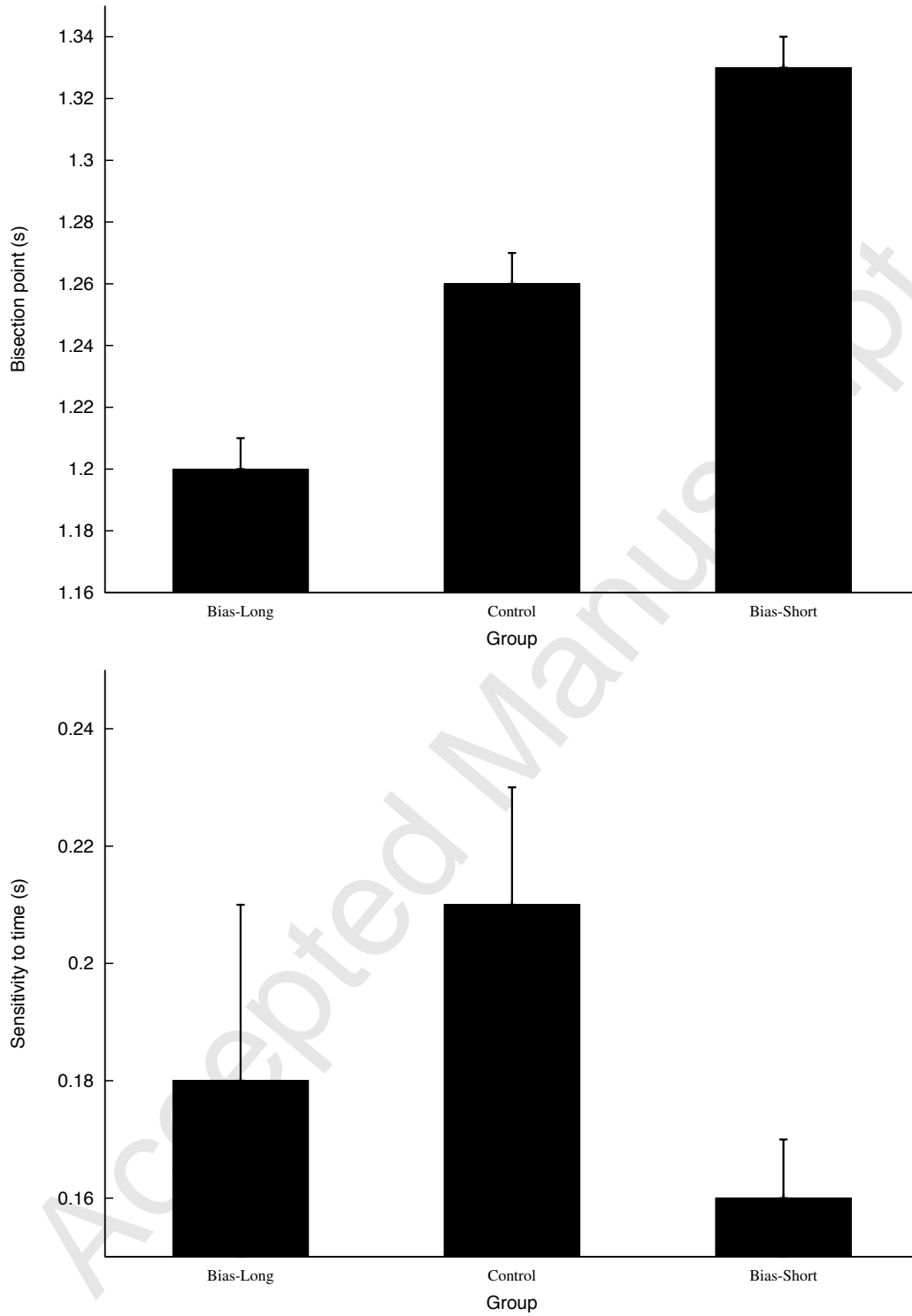
Figure 5. Top panel: Fit of SET to the data (points). $b = 1.05$, $k = 0.18$. Bottom panel: Fit of BEM to the data (points). $b = 1.50$, $k = 0.18$.
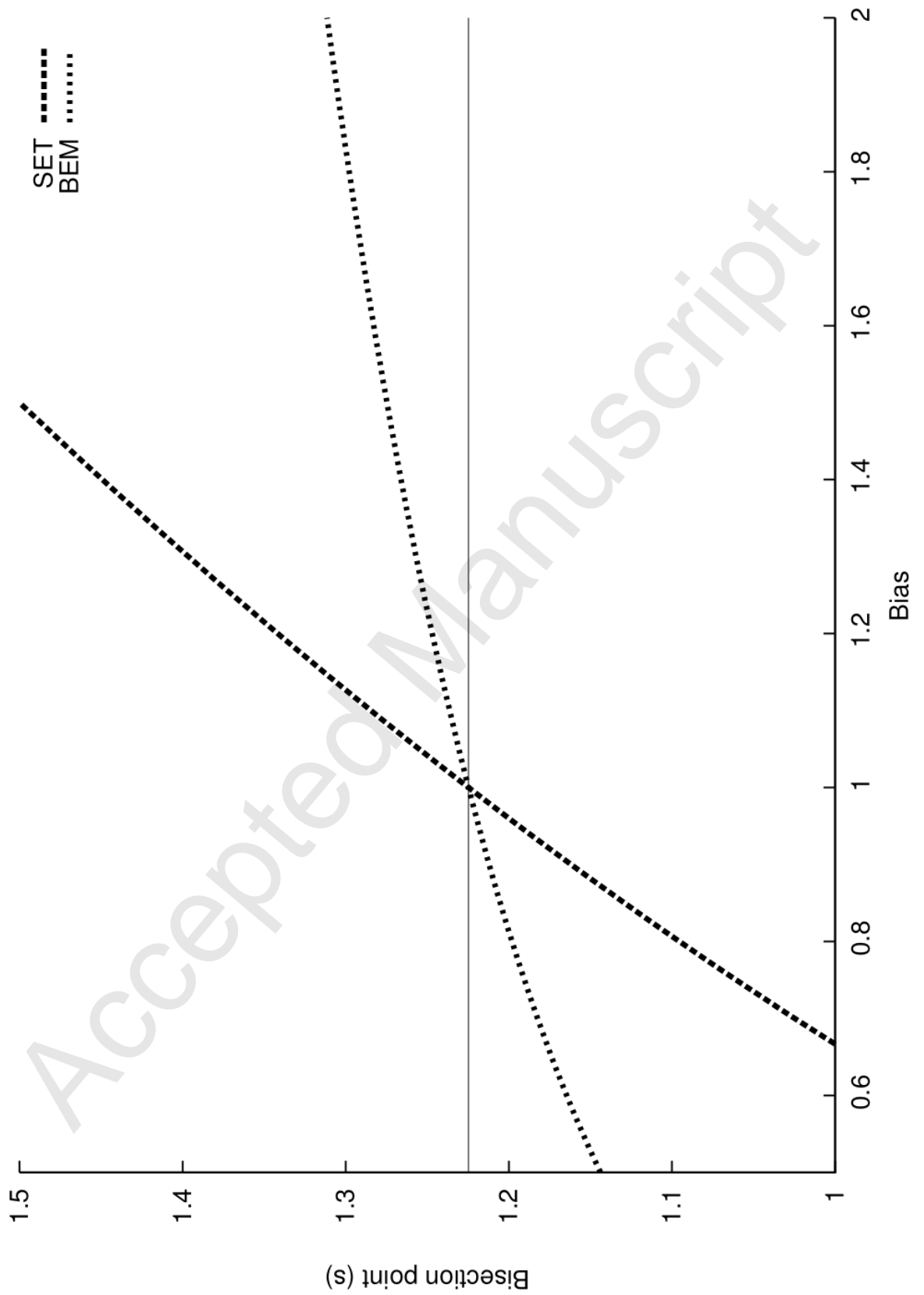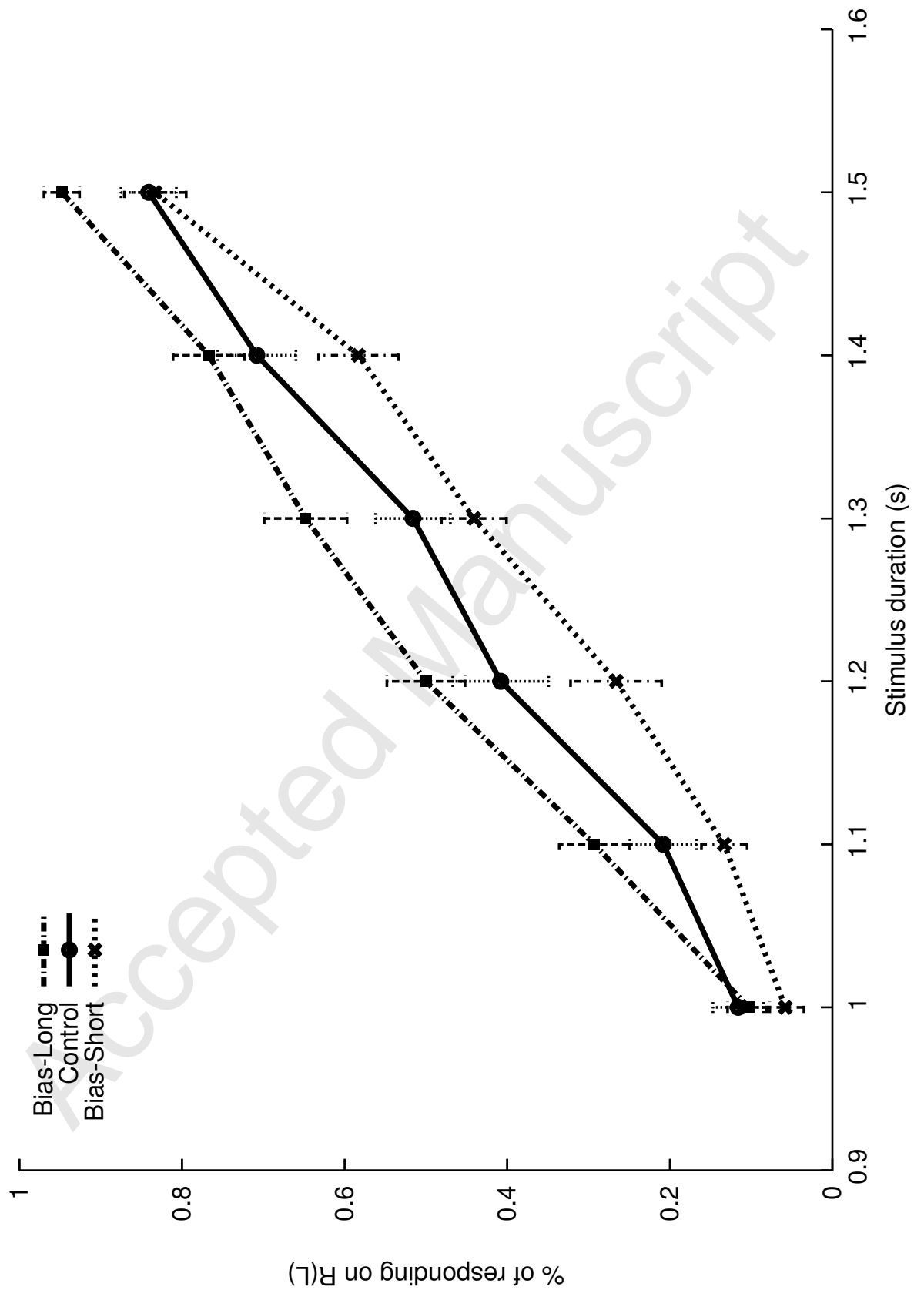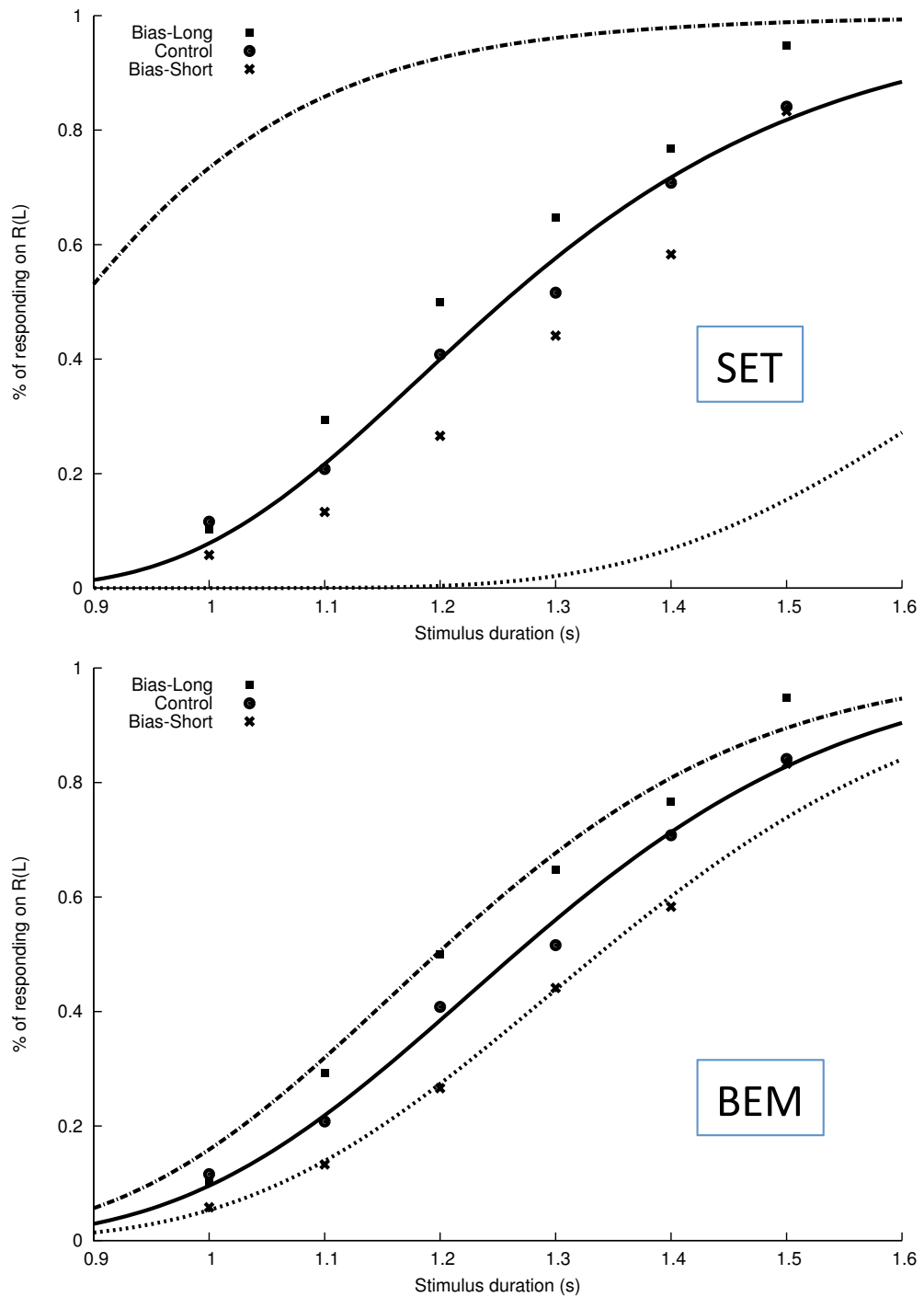
Jozefowiez, Pollack, Machado, & Miller, Figure 1
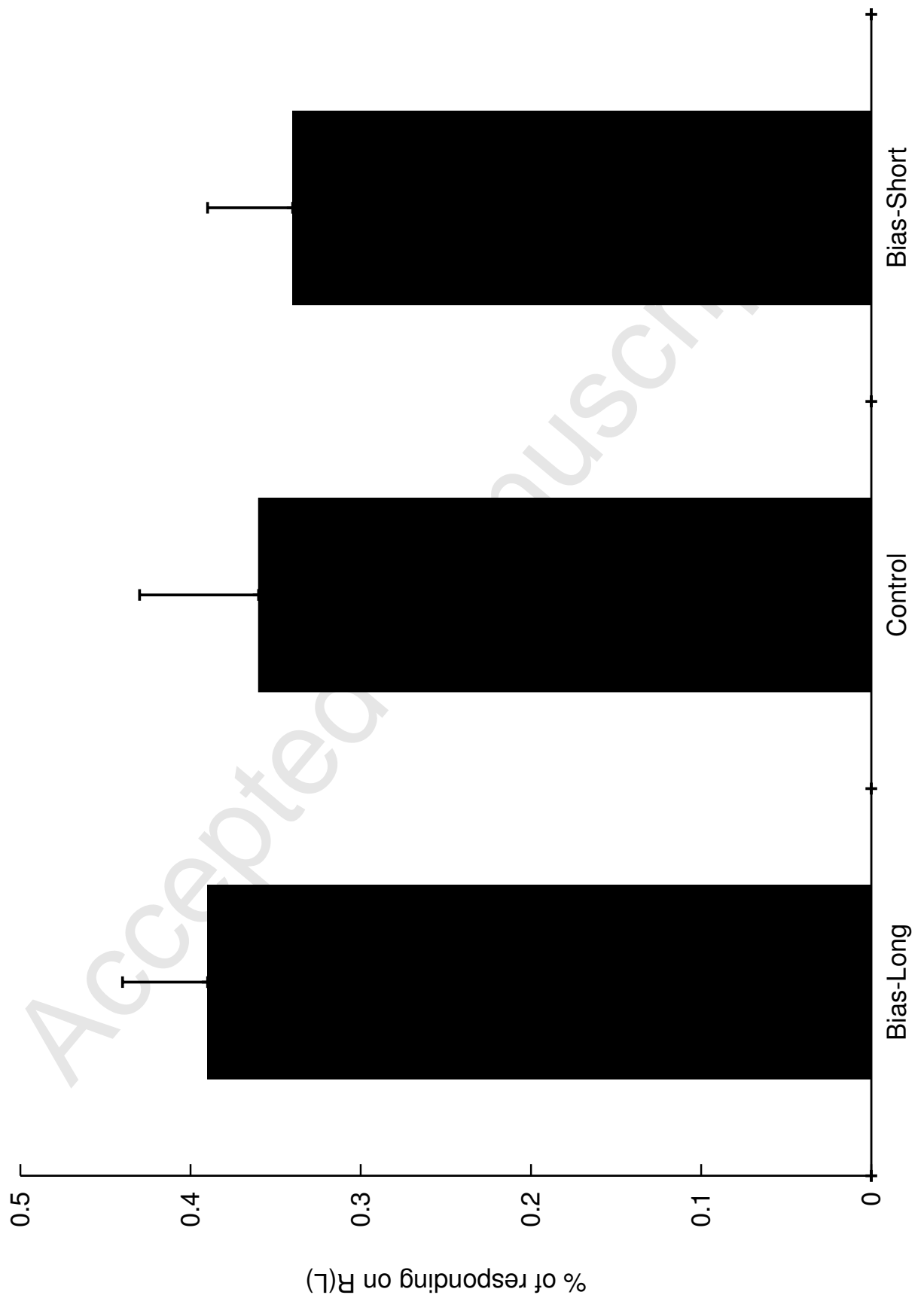
Jozefowiez, Pollack, Machado, & Miller – Figure 2

Jozefowiez, Polack, Machado, & Miller- Figure 3

Jozefowiez, Polack, Machado, & Miller- Figure 4

Jozefowiez, Pollack, Machado, & Miller – Figure 5

- Participants are exposed to a bisection task in which trial frequency of each stimulus duration is manipulated.
- Participants show a bias toward the response associated with the more frequent duration
- The size of the bias effect is more consistent with the Behavioral Economic Model than with the Scalar Expectancy Theory.