

Effects of Skewed Probe Distributions on Temporal Bisection in Rats: Factors in the
Judgment of Ambiguous Intervals

by

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ABSTRACT

Temporal bisection is a common procedure for the study of interval timing in humans and non-human animals, in which participants are trained to discriminate between a “short” and a “long” interval of time. Following stable and accurate discrimination, unreinforced probe intervals between the two values are tested. In temporal bisection studies, intermediate non-reinforced probe intervals are typically arithmetically- or geometrically-spaced, yielding point of subjective equality at the arithmetic and geometric mean of the trained anchor intervals. Brown et al. (2005) suggest that judgement of the length of an interval, even when not reinforced, is influenced by its subjective length in comparison to that of other intervals. This hypothesis predicts that skewing the distribution of probe intervals shifts the psychophysical function relating interval length to the probability of reporting that interval as “long.” Data from the present temporal bisection study, using rats, suggest that there may be a within-session shift in temporal bisection responding which accounts for observed shifts in the psychophysical functions, and that this may also influence how rats categorize ambiguous intervals.

DEDICATION

This work, and all my work, is first and foremost dedicated to my parents, Anupama and Ajay Gupta, who have supported my scientific curiosity since I was young, and to whom I dedicate my academic middle initial. Natasha Gupta for always providing humor and perspective, and Zakary Marquez for constant support, encouraging conversation, and countless rides to and from the lab. My mentor, Dr. Federico Sanabria for introducing me to this great field of research and for giving me the opportunity to run the Basic Behavioral Processes Lab. Dr. Clive Wynne and Dr. Mike McBeath for enlightening discussions regarding my data and its interpretation. My former labmates, Dr. Carter Daniels and Cristina Dos Santos for comradery and mentorship during my first year of graduate school. Finally, to my colleagues in the ASU Behavioral Neuroscience program, who are a constant source of knowledge, inspiration, and friendship.

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CHAPTER 1

INTRODUCTION

Much of an animal's ability to organize its behavior is dependent upon its capacity to perceive intervals of time in the minutes-to-seconds range. Without this capacity, activities such as foraging for food and avoiding predation would likely be inefficient and ineffective (Meck & Buhusi, 2005). Additionally, interval timing is widely implicated across psychopathologies, with timing deficits observed in autism (Falter, Noreika, Wearden, & Bailey, 2012), attention-deficit hyperactivity disorder (ADHD; Smith et al., 2004), schizophrenia (Ward, Kellendonk, Kandel, & Balsam, 2012), and Alzheimer's disease (Caselli, Iaboli, & Nichelli, 2009). Because it concerns time estimation processes which are implicated in decision-making (Meck & Buhusi, 2005), studying the experimental and contextual manipulations which have bearing on interval timing provides insight into the cognitive processes that underlie the ability to respond to the environment in an effective and productive manner.

The temporal bisection procedure is a standard method of investigating interval timing. In a temporal bisection experiment in animal models, one response (e.g., left lever press) is reinforced after a short interval (e.g., 2 s), and another response (e.g., right lever pressing) is reinforced after a longer interval (e.g., 8 s). After learning this discrimination, intermediate intervals (probes) between the two anchor intervals are presented without reinforcement. Performance is then represented as a psychophysical function that relates the probability of pressing the lever associated with the long interval [p ("long")] to the length of time intervals. Based on this function, the point of subjective equality (PSE)—the interval at which p ("long") is approximately .5—is calculated. Inferences on the

mechanisms that underlie the temporal control of behavior may be drawn from the shape and position of the psychophysical function as well as from the PSE.

CHAPTER 2

REVIEW OF THE LITERATURE

While the psychophysical function and PSE obtained from temporal bisection performance are sensitive to a range of variables including rate of reinforcement and anchor lengths (Akdoğan, B., & Balci; Araiba & Brown, 2016; Church & Deluty, 1977; Killleen & Fetterman, 1988; Machado, 1997; Raslear, 1985; Wearden & Ferrara 1995), probe spacing is an especially salient variable in temporal bisection performance. When probes are arithmetically spaced (constant difference between consecutive intervals; Allan & Gibbon, 1991; Wearden & Ferrara, 1995) or logarithmically spaced (geometrically growing difference between consecutive intervals; Allan, 2002; Allan & Gibbon, 1991; Rakitin et al., 1998), the PSE is typically located between the arithmetic and geometric mean of the anchors. Additionally, even when data are derived from diverse anchor lengths, normalization by the geometric mean can account for the majority of variance in PSEs derived from logarithmically spaced probes (Church & Deluty, 1977).

Despite the apparent prevalence of the geometric mean of anchors as the PSE, when the arithmetic and geometric means of the anchors are explicitly presented to human subjects in arithmetically or logarithmically spaced distributions, neither value yields completely evenly distributed “short” and “long” responses (Wearden & Ferrara, 1995). This effect is also dependent upon probe spacing: the PSE is more often the geometric mean of anchors when probes are geometrically spaced, compared to when the probes are arithmetically spaced (Killleen & Fetterman, 1988; Raslear, 1983; Wearden & Ferrara, 1995). Effects of probe distribution are also observed in the shape of the

psychophysical function. Logarithmic series of probes result in a leftward shift of the psychophysical function compared to arithmetic series of probes, which may reflect a decrease in the rate of reinforcement (longer mean probe interval) in the arithmetic probe series (Fetterman, Killeen, & Evans, 1986; Killeen & Fetterman, 1988).

Despite its apparent influence on temporal bisection performance, major theories of timing often omit making predictions about the effect of probe spacing, as there is a general assumption that probes intervals are sampling from an underlying psychophysical function, and thus, the specific samples should not have bearing on responding (Gibbon, 1977; Killeen & Fetterman, 1988). Predictions and variations in the psychophysical function and its PSE due to procedural differences suggest that responses to a given interval in temporal bisection tasks may not be indicative of only perception of that given interval's length, but that this value may also be sensitive to other intervals presented in the same experimental context. This idea is evidenced by double bisection experiments in pigeons (Machado & Pata, 2005; Machado & Arantes, 2006; Maia & Machado, 2009). In this procedure, pigeons were trained to associate a red and green key with 2-s and 8-s intervals, respectively, and then trained to associate a vertical bar and horizontal bar with 4-s and 16-s intervals, respectively (Maia & Machado, 2009). When exposed to a 4-s interval and given a choice between red and green keys, pigeons show bias towards red, suggesting that pigeons learn not only the absolute length of intervals, but also their relation to other intervals.

Effect of Probe Distribution in Temporal Bisection

The effect of probe distribution in temporal bisection was well demonstrated by Brown et al. (2005), who examined the sensitivity of PSEs to probe distribution and

anchor ratio in humans, using extremely positively skewed (superlogarithmic) and extremely negatively skewed (antilogarithmic) probe distributions, as well as small and large anchor ratios. Positively-skewed probes yielded left-shifted psychophysical functions with lower PSEs than negatively-skewed probes, and this effect increased as the ratio between the short and longer anchor increased (Brown et al., 2005).

Brown and colleagues suggest that, insofar as the judgement of an interval is in some way influenced by its subjective magnitude relative to the endpoints (anchors), the same principles which apply to the judgment of non-temporal stimuli, should apply to intervals of time. This is the basis for temporal range frequency theory (TRFT; Brown et al. 2005), which suggests that judgement of intervals by humans in temporal bisection can be skewed in the direction of the distribution in which they are presented. This implies that the humans may learn the underlying distribution of probe intervals, and that this is reflected in the pattern of judgments.

Research Aims and Hypotheses

Overall, the sensitivity of the psychophysical function in temporal bisection to probe distribution and anchor ratio is of substantial interest to interval timing research, as it suggests that animals time not only the occurrence of significant events (anchors), but also continue to engage in timing during the absence of those events (probes). The purpose of the current project is to examine the effect of probe distribution and anchor ratio in rats, and to test whether Brown et al.'s findings generalize to this species. Use of rats affords a large amount of timing data obtained under strictly controlled conditions. Further, such data will inform whether animals' responses in temporal bisection tasks are

sensitive to the context in which questions about intervals are posed to them, rather than to just the intervals themselves.

In order to examine these effects, eight adult Sprague Dawley male rats were trained on a temporal bisection task, in which they were trained to discriminate between two different intervals of time, and were tested on skewed distributions of probes in two different anchor ratios: skewed-long (majority of probes near long anchor) and skewed-short (majority of probes near short anchor). Additionally, in order to test the effects of the skewed probe distribution on performance at ambiguous intervals, a common probes phase was implemented, wherein the animals were tested on the arithmetic mean, geometric mean, and small and large extreme values of each anchor ratio. A follow-up study was also conducted in which probe intervals greater than or less than the geometric mean of the anchor ratio were eliminated, in order to examine whether effects at ambiguous intervals could be strengthened in this manner.

CHAPTER 3

METHODS & MATERIALS

Subjects

Eight male Sprague-Dawley rats (Charles River Laboratories, Hollister, California) served as subjects. Rats arrived on post-natal day (PND) 104, and were pair housed upon arrival. Rats were housed in a 12:12 h light cycle, with lights on at 1900 h. Behavioral training and testing was always conducted in the dark phase of the light cycle. Shortly after arrival, rats began behavioral training and food deprivation. Daily food access was progressively reduced from 24, to 18, 12, 6, 3, and then 1 h/day. Food was placed in the chow hopper of the cages during the dark phase of the light cycle. During all phases of behavioral training, rats were fed 30 min after the conclusion of each training or testing session. Weights immediately prior to the experimental sessions were maintained at 75% of mean *ad libitum* feeding weights, as estimated from growth charts from the breeder. Rats had *ad libitum* access to water in their home cages. On Day 43 of the experiment, one rat was euthanized following accidental injury. This animal's data up until its death was included in analyses. All animal handling procedures in this study followed National Institutes for Health Guidelines and were approved by the Arizona State University Institutional Animal Care and Use Committee.

Apparatus

Behavioral training and testing were conducted in 8 Med Associates (St. Albans, VT, USA) modular test chambers (305 mm long, 241 mm wide, and 210 mm high). Each chamber was enclosed in a sound- and light- attenuating cabinet equipped with a ventilation fan, which provided mask noise of ~60 dB. Each box had front and back walls

made from Plexiglas. The front door had a hinge and served as the door for the chamber. One of the aluminum side panels served as the test panel. The floor was composed of thin metal bars mounted above a catch pan. The reinforcement port was a square opening (51 mm per side), positioned 15 mm above the chamber floor. The port provided access to a liquid dipper (MED Associates, ENV-202M-S), which was fitted with a cup (MED Associates, ENV-202C) that held up to 0.01 cc of a liquid reinforcer (33% sweetened condensed milk, by volume, diluted in tap water; Kroger brand, Cincinnati, OH). The port had a head entry detector (ENV-254-CV). A multiple tone generator (MED Associates, ENV-223) could produce a 15-kHz tone through a mounted speaker (MED Associates, ENV-224AM), positioned in the center of the wall opposite the test panel, 240 mm above the chamber floor. Two retractable levers (ENV-122CM) flanked the reinforcement port. Lever presses with a force of 0.2 N at the end of the lever were recorded. A houselight on the wall opposite to the test panel was used to indicate an ongoing interval. Experimental events were programmed in MedState Notation[®], controlling a MED-PC IV[®] interface running on Windows XP.

Experiment 1

Design

Four variations of the temporal bisection task were implemented in a fully-counterbalanced 2×2 (anchor-ratio \times probe distribution) factorial within-subject design. All rats first experienced the same pre-training conditions and were then assigned to one of two anchor-training groups ($n = 4$ each). One group was trained to discriminate 2-s vs. 8-s anchor intervals (small, 1:4 anchor ratio); the other group was trained to discriminate 2-s vs. 24-s anchor intervals (large, 1:12 anchor ratio). Rats in each anchor-training group

were then assigned to one of two probe-distribution groups, counterbalancing anchor-discrimination performance. One group was tested using a skewed-short (positively-skewed; most probes close to short anchor) probe distribution; the other group was tested using an skewed-long (negatively-skewed; most probes close to long anchor) probe distribution. Both groups were then tested using a common distribution of probes. Probe-distribution assignment was then switched; rats were tested on a new probe distribution and then again on the common probe distribution. Finally, anchor-training was reinstated with group assignment switched, and testing on skewed-short, skewed-long, and common probes was conducted again as described. Table 1 describes the order of training and testing conditions for each of the four groups. The whole study took 154 days to complete. All training and testing sessions lasted 60 min, including a 3-min acclimation period, during which no stimuli or manipulanda in the chamber were activated.

Reinforcer Consumption Training

Prior to training on the bisection task, all rats were trained to consume the reinforcer (sweetened condensed milk) from the liquid dipper in the reinforcement port. Following the 3-min acclimation period, a reinforcer was made available at the liquid dipper. All subsequent reinforcers were made available at variable intervals, with a mean inter-trial interval (ITI) of 45 s. During the ITI, no stimuli or manipulanda were activated. When a reinforcer was delivered, the houselight turned on and the liquid dipper was activated. Head entries into the reinforcement port activated a 15-kHz tone. The dipper and tone were deactivated 2.5-s after the head entry. Reinforcer consumption training continued for seven days, until rats received 100 reinforcers per session and the median time to retrieve reinforcement was 4 s or less.

Lever Training

Following reinforcer consumption training, rats were trained to lever press for the reinforcer. This was a modification of the reinforcer consumption training, wherein after the acclimation period, one of the response levers was extended. Pressing the lever retracted it into the test panel, activating the liquid dipper and a 15-kHz tone. A head entry into the reinforcement port initiated a 2.5-s interval, after which the dipper and tone were deactivated and a 5-s ITI was initiated. Which lever (left or right) was extended on a given trial was determined pseudo-randomly by sampling from a 6-item list, such that the same lever would not be activated more than 6 times in a row. Lever training continued for seven days, until all rats were reliably pressing levers for at least 100 trials/session.

Anchor Training

Rats were then trained to discriminate between two anchor intervals. The beginning of an interval was signaled by the houselight turning on; the end was signaled by the houselight turning off. Following the acclimation period, the chamber houselight was turned on, remaining activated for the duration of either the short (2 s) or long (8 s in small-ratio condition; 24 s in large-ratio condition) anchor. In all trials, the anchor interval was selected pseudo-randomly by sampling without replacement from a 6-item list, such that the same interval would not be selected more than 6 times in a row. After the interval had elapsed, the houselight turned off, and both levers on the test panel were extended. The left lever was associated with the short interval for four rats, and with the long interval for the remaining four rats. When the rat pressed one of the levers, a correct choice was marked by a 15-kHz tone, which was deactivated by a head entry into the reinforcement port. The dipper was deactivated 2.5 s after the head entry, followed by a

5-s ITI. Incorrect choices were followed by a 10s ITI during which no stimuli or manipulanda were activated. Anchor interval training continued until mean $p(\text{correct}) \geq 0.80$ for five consecutive days in the short-ratio conditions, and for 10 consecutive days in the long-ratio condition (to equate the number of trials being assessed between conditions). Stability in performance was confirmed by a non-significant linear regression of $p(\text{correct})$ over those days. Anchor interval training took 14 days.

Distributed Probe Testing

After anchor discrimination performance stabilized, rats were tested on eight intermediate probe durations, presented in either a positively-skewed (skewed-short) distribution, where most probes were relatively short, or in a negatively-skewed (skewed-long) distribution, where most probes were relatively long. Table 2 shows the probes in each distribution, as calculated using Equations 1 and 2 (Appendix A), where L is the long anchor, S is the small anchor, I is ordinal position of the probe interval ($I = 1$ for the shortest probe; $I = 8$ for the longest probe), and n is the total number of probe intervals ($n = 8$). These equations were derived in Wolfram Mathematica using the probe interval distributions provided by Brown et al. (2005).

Probe testing sessions were arranged in blocks of 16 trials. In each block, 8 trials were anchors (4 short, 4 long), and 8 were intermediate probe intervals. Correct responses after anchor intervals were reinforced as before; responses after probe intervals were not reinforced—they just initiated a 7.5-s ITI. Intervals were selected pseudo-randomly by sampling without replacement from a 16-item list. Skewed-short and skewed-long probe testing continued for 15 days in each condition; stable discrimination of the anchors was assessed as before.

Common Probe Testing

Following skewed-short and skewed-long probe testing, rats were tested on the mean and extreme values in their assigned anchor-ratio condition, as described in Table 3. Each common probe testing session was arranged in two stages. The first stage was identical to the distributed probe testing condition but lasted only 132 trials in the small-ratio condition and 70 trials in the large-ratio condition. These were half of the minimum number of trials completed by any rat in a session during the distributed testing phase in the corresponding anchor-ratio condition. Once these trials were completed, the common probes testing procedure was implemented for the remainder of the session.

Common-probes testing was arranged in blocks of 16 trials. Just as before, 8 trials were reinforced anchors intervals and 8 trials were intermediate non-reinforced probe intervals; trials were selected pseudo-randomly by sampling without replacement from a 16-item list. Unlike the previous phase, however, the probe intervals included the shortest skewed-short interval, the geometric mean of the anchors, the arithmetic mean of the anchors, and the longest Skewed-long interval (Table 3). Common probe testing took place over 5 days. In order to equate the number of common-probe trials between anchor-ratio conditions, rats in the large-ratio condition were tested on common probes on days 1, 2, 4, and 5, and rats in the short-ratio condition were tested on common probes only on days 1 and 3. All other days consisted only of skewed-short or skewed-long probes, just as in the previous phase.

Experiment 2

Subjects and Apparatus

Eight male Sprague-Dawley rats (Charles River Laboratories, Hollister, California) served as subjects. Rats arrived on post-natal day (PND) 104, and were pair housed upon arrival. Rats were housed in a 12:12 h light cycle, with lights on at 1900 h. Food restriction was implemented in the same manner as in Experiment 1. All animal handling procedures in this study followed National Institutes for Health Guidelines and were approved by the Arizona State University Institutional Animal Care and Use Committee. Operant chambers and reinforcement were identical to those used in Experiment 1.

Design

Three variations of the temporal bisection task were implemented for each rat in counterbalanced order. Animals were all pre-trained as in Experiment 1. They were then trained to discriminate 2-s vs. 24-s anchor intervals. Following stable and accurate anchor discrimination, all animals were tested in a baseline condition, using geometrically-spaced probes. Rats were then assigned to one of two biased probe-testing groups ($n = 4$), counterbalancing anchor-discrimination performance. One group was tested using *biased-short* probes, where all probes greater than the geometric mean of the anchor ratio (6.93 s) were eliminated; the other group was tested using *biased-long* probes, where all probes less than the geometric mean of the anchor ratio were eliminated.

Following stable responding in these conditions, rats were re-tested in the baseline condition, again using the full set of geometrically-spaced probes. Following stable responding, biased probe-testing conditions were switched and conducted again as described. Table 6 describes the order of training and testing conditions for each group. This experiment took 94 days to complete. All training and testing sessions lasted 60 min,

including a 3-min acclimation period during which no stimuli or manipulanda in the chamber were activated.

Pretraining.

Reinforcer consumption training, lever training, and anchor training (2-s vs. 24-s) were conducted as in Experiment 1.

Baseline Probe Testing

After anchor discrimination performance stabilized, rats were tested on nine intermediate probe durations, presented in either a geometrically-spaced distributions. Table 7 shows the probes in each distribution.

Probe testing sessions were arranged in blocks of 17 trials. In each block, 4 trials were small anchors (2-s), 4 were long anchors (24-s), and 9 were intermediate probe intervals. Correct responses after anchor intervals were reinforced as before; incorrect responses and responses after probe intervals were not reinforced—they just initiated a 7.5-s ITI. Intervals were selected pseudo-randomly by sampling without replacement from a 17-item list. Probe testing continued for 15 days in this condition, and stability on anchor responding were assessed as before.

Biased Probe Testing

After performance in baseline probe testing stabilized, rats were tested in the two biased probes condition, in which all intervals greater than or less than the geometric mean (bias-short and biased-long, respectively) were eliminated, in counterbalanced order (Table 7). Biased probe testing sessions were arranged just as in baseline probe testing, but each remaining probe, other than 6.93-s, was presented twice per block rather than once per block.

CHAPTER 4

RESULTS

Experiment 1

Data Analysis

Data from the last five sessions of the distributed probes phase and from all common-probe trials were analyzed. Psychophysical functions for each anchor-ratio \times probe-distribution condition were drawn using the mean proportion of “long” responses across sessions for each interval ($p(\text{“long”})$). PSEs for each animal were estimated using linear interpolation of the psychophysical function in each condition. Linear interpolation was chosen over other methods of PSE estimation because it does not assume the shape of the psychophysical function (Wearden & Ferrara, 2007). Bayesian t-tests were conducted to compare the mean log-transformed PSEs between distributed probe condition. Bayesian t-tests were chosen because they reduce the influence of outliers and missing data, while also allowing for comparison between the null and alternative models.

For the common-probes phases, $p(\text{“long”})$ was computed for each interval to construct a psychophysical function, and these were compared between probe-distribution conditions. Because the majority of bisection experiments yield PSEs between the geometric and arithmetic means of the anchor ratio, mean $p(\text{“long”})$ at these intervals was expected to be particularly sensitive to probe-distribution effects. Bayesian t-tests were conducted to compare mean log-odds of “long” responses, $\ln[(p(\text{“long”})/(1 - p(\text{“long”})))]$, to each common-probe interval. Bayesian t-tests were also conducted to compare mean PSEs between distributed probe condition.

Psychophysical Functions in Distributed Probes Testing

Figure 1 shows the mean psychophysical functions for each distributed-probes testing condition, as well as a comparison between psychophysical functions of skewed-long and skewed-short conditions within the same anchor-ratio condition. In both the small and large anchor-ratio conditions, the psychophysical function appears to be shifted left for the skewed-short distributed probes compared to the skewed-long probes. This shift appears to be larger in the large anchor-ratio condition than in the small anchor ratio condition.

In addition to calculating p (“long”) for each interval, p (“long”) across all intervals was also analyzed (p (“long”| all). In the small ratio condition, mean log-odds of p (“long”| all) is significantly higher for the skewed-long distributed probes ($M = 0.622$, $SEM = 0.19$) than for the skewed-short distributed probes ($M = -0.577$, $SEM = 0.26$), $\text{Log}(BF_{10}) = 4.970$. For the large ratio condition, mean log-odds of p (“long”| all) for the skewed-long distributed probes ($M = 1.40$, $SEM = 0.18$) is increased compared to that for the skewed-short distributed probes, ($M = -0.766$, $SEM = 0.20$), $\text{Log}(BF_{10}) = 23.48$.

PSEs in Distributed Probes Testing.

Figure 2 compares mean PSEs between skewed-long and skewed-short probe distributions in the small and large anchor ratio conditions. For the small anchor ratio, the skewed-long distributed probes yielded mean PSE = 4.08 +/- 0.65 s, and skewed-short distributed probes yielded mean PSE = 3.84 +/- 0.20 s. In this condition, a Bayesian t-test indicated that there is not strong evidence for the alternative hypothesis ($\text{Log}(BF_{10}) = -0.156$). For the large anchor ratio, the skewed-long yielded PSE = 6.58 +/- 0.24 s and skewed-short distributed probes had PSE = 4.80 +/- 0.17 s. In this condition, there is

strong evidence that the PSE is significantly higher in the skewed-long condition than in the skewed-short condition ($\text{Log}(BF_{10}) = 1.46$).

Common Probes

Figure 3 shows the mean psychophysical functions for the common probes following each distributed-probes condition. The psychophysical functions of common probes appear to be shifted down (lower p (“long”)) following the skewed-short condition, compared to the skewed-long condition (higher p (“long”)). This shift appears to be larger in the large anchor ratio condition.

The common probes revealed that animals that had experienced a positively-skewed (skewed-short) distribution were more likely to report the arithmetic and geometric mean as “short” than those that had experienced a negatively-skewed (skewed-long) distribution (Figure 3), indicating a trend opposite to that which was observed in the distributed-probes condition (Figure 1). Notably, whereas the common probes functions following skewed-long probes remains relatively unshifted, the common probes function following skewed-short probes is shifted down.

Tables 4 and 5 show a summary of Bayesian t-test comparisons between the common probes in the skewed-short and skewed-long distributed probes conditions. In both the small and large anchor-ratio conditions, strong evidence for a difference in the log-odds of p (“long”) was observed only at the arithmetic mean, such that rats were more likely to report this value as “long” in the skewed-long condition than in the skewed-short condition, and this effect was greater in the large-ratio condition than in the small-ratio condition.

Experiment 2

Data Analysis

Data from the last five sessions from each baseline and biased-probes condition and were analyzed. Data from the first and second baseline conditions were combined, as baseline performance did not differ systematically between the two phases.

Psychophysical functions for each condition were drawn using the average $p(\text{“long”})$ for each interval, which was calculated by taking the proportion of “long” responses to total responses.

Of particular interest in this experiment was the probability of responding “long” when the geometric mean of the anchors was presented [$p(\text{“long”} \mid \text{GM})$]. This parameter was compared across baseline and biased-probes conditions. Bayesian t-tests were conducted to compare mean log-odds of “long” responses, $\ln[(\text{mean } p(\text{“long”}) / (1 - \text{mean } p(\text{“long”})))]$ between bias conditions. Bayesian t-tests were also conducted to compare mean PSEs between baseline conditions. Difference in the log-odds of $p(\text{“long”} \mid \text{GM})$ between baseline and bias conditions were also analyzed in this manner.

Biased Conditions

Figure 4 shows the psychophysical functions for $p(\text{“long”})$ for each interval for the bias-short and bias-long conditions. There is no apparent shift in the psychophysical functions based on biased conditions. Bayesian t-tests on the mean log-odds for the last five sessions for $p(\text{“long”} \mid \text{all intervals})$ revealed strong evidence for an effect of bias condition such that animals categorized intervals as “long” significantly more frequent in the bias-long condition ($M = 0.522$, $\text{SEM} = 0.122$) than in the bias-short condition ($M = -0.355$, $\text{SEM} = 0.053$), ($\text{Log}(BF_{10}) = 7.05$). This observation confirms that the animals did indeed bias their responding in the direction of the presented probes.

Effect of Probe Bias on p (“long” | GM)

Figure 5 shows the mean difference from baseline of the log-odds of p (“long” | GM) for the bias-short and bias long conditions. Although Figure 5 suggests that judgement of the GM may have been biased in the direction of the probe bias, a Bayesian t-test revealed evidence for the null hypothesis ($\text{Log}(BF_{10}) = -0.328$). This indicates that with the current experimental parameters, eliminating probes greater and less than the GM was not sufficient to significantly influence responding to an ambiguous interval.

CHAPTER 5

DISCUSSION

Overview of Results

In Experiment 1, rats trained on a temporal bisection task with skewed probe distributions showed temporal judgments parallel to those observed in humans by Brown et al. (2005), where testing with skewed-short (positively-skewed) probes induced a leftward shift in the psychophysical function, such that animals categorized shorter intervals as “long” more frequently. Because the skewed-long and skewed-short distributions contain distinct probes which cannot be directly compared, the common probes test was conducted as a means to compare responding following exposure to the skewed distributed probes. Additionally, the common probes can be considered a test of implicit learning of the skewed distributions during distributed probes testing, and the extent to which this is reflected in their response to the mean and extreme values of those distributions.

For the small anchor ratio in the common probes test, the arithmetic mean was reported as “long” significantly less often following the skewed-short distributed probes than following the skewed-long distributed probes. This effect of probe spacing on judgment of the arithmetic mean was enhanced in the large anchor ratio.

Experiment 2 examined whether the frequency of long or short intervals within a distribution in temporal bisection biases the categorization of ambiguous intervals. This was done by training animals on a temporal bisection task with geometrically-spaced probes. Following this, animals were tested on biased probe distributions, in which all intervals in the geometric sequence greater than or less than the geometric mean were

removed. Following from the results of the common probes test in Experiment 1, it was predicted that judgment of the GM would be shifted in the direction of the probe bias, such that animals would be more likely to categorize the GM as “short” when more short probes were presented, and more likely to categorize the GM as “long” when more long probes are presented. Analysis of the psychophysical functions and judgment of the GM in Experiment 2 did not support these predictions, and judgment of the GM was not significantly biased by modifying the frequency short or long probes.

A Behavioral Account of the Influence of Skewed Probes on Temporal Bisection

Psychophysical functions from the skewed-short and skewed-long probes appear to be consistent with predictions from TRFT (Brown et al., 2005; Figures 1 and 2), as the functions appear to be shifted in the direction of the probe skews. That is, when the majority of the probes are close to the small anchor, animals are more likely to categorize shorter intervals as “long,” and when the majority of probes are close to the long anchor, animals are more likely to categorize longer intervals as “short.”

The Learning to Time theory (LeT; Machado, 1997) predicts such differences in the psychophysical function as a result of differential probe spacing. LeT describes timing as a serial activation of behavioral states as time progresses. During an interval, as this activation of states progresses, the associative strength between a given state and a *reinforced* response increases. Conversely, the association between a given state and an unreinforced response is weakened (Machado, 1997). Thus, insofar as unreinforced responses to probes which are close to an anchor weaken the “short” response and strengthen the “long” response, LeT predicts that, relative to arithmetically-spaced

probes, unreinforced logarithmically-spaced probes would induce a rightward shift the psychophysical function (Machado, 1997; Machado, Malheiro, Erlhagen, 2009).

Contrary to what was suggested by Brown et al. (2005), who invoked cognitive range-frequency principles to account for the shifted psychophysical functions in temporal bisection with skewed probes, the observed pattern of results in the current study can largely be replicated by implementing an LeT-like state-based behavioral model of interval timing. This can provide a comparatively simple behavioral account of stimulus spacing effects in temporal bisection in rats, based only on the relative association of the “long” and “short” choices with behavioral states activated while a given interval elapses. Thus, when animals are tested with skewed probe distributions, choices associated with states similarly activated by anchors (“short” in positively-skewed distributions and “long” in negatively-skewed distributions) would be strengthened as the session progresses.

This could account for the observed “flip” in psychophysical function between the distributed probes and within-session common probes test by strengthening “short” and “long” choices for positively- and negatively-skewed distributions, respectively, as the session progresses. It is important to note, however, that this model is reliant on the modification of the relative probability of the “short” and “long” choices by feedback, and therefore may not be applicable in human studies, which often ask participants to judge to the probes relative to the short and long anchors in the absence of any reinforcement or feedback.

State-based Model of Interval Timing

In order to test this behavioral account of the observed results, data were modeled using a Monte Carlo simulation of a *state-based model of interval timing*. This model is a simplified version of LeT (Machado, 1997). It similarly assumes that, in the time following reinforcement, animals progress through a series of behavioral states, each differentially associated to each choice (Machado, 1997; Machado, Malheiro, & Erlhagen, 2009). Figure 6 describes the schematic of the simulator. All simulations were conducted in Wolfram Mathematica (Wolfram Solutions, Champaign, IL).

The model assumes a vector of states, $S(1), S(2), S(3)\dots$, where each state has a corresponding probability of responding “long”, $p(1), p(2), p(3)\dots$. At the beginning of each run, all elements in the probability vector were seeded at .5. Each run consisted of 3000 trials. Each trial started by (a) randomly sampling without replacement an interval T from a list, just as in the simulated experimental condition (e.g., biased-long: 2.00 s, 6.93, 8.88 s, etc.), (b) setting a trial timer $t = 0$ s and a state counter $n = 1$, (c) activating state $S(n)$, (d) sampling a state-dwelling interval i from an exponential distribution with mean c , and (e) adding i to timer t . If $t < T$, n increased by 1 and steps (c) through (e) were repeated. Once $t \geq T$, a “long” response was produced with probability $p(n)$ and the trial was finished. Before starting the next trial, $p(n)$ was updated according to the following rules:

- (1) If “long” response was reinforced, $p(n) \leftarrow p(n) + R[1 - p(n)]$
- (2) If “short” response was reinforced, $p(n) \leftarrow p(n) + R[0 - p(n)]$
- (3) If “long” response was extinguished, $p(n) \leftarrow p(n) + E[0 - p(n)]$
- (4) If “short” response was extinguished, $p(n) \leftarrow p(n) + E[1 - p(n)]$

Rules 1 and 2 apply only when the long and short anchor, respectively, are correctly identified; Rule 3 applies when any interval other than the long anchor is identified as “long”; Rule 4 applies when any interval other than the short anchor is identified as “short.”

Figure 7 shows the implementation of the state-based interval timing model to simulate the effect of skewed probe distributions, compared to the experimental data. Psychophysical functions from simulations were drawn based on p (“long”) computed for each interval based on all responses. The attained curves show the characteristic shift in function induced by the skewed probes.

Within-Session Effects in Temporal Bisection

Taken together, results of Experiments 1 and 2 suggest that, with the current experimental parameters, inducing a categorization bias by increasing the proportion of “long” or “short” intervals within a probe distribution was not sufficient to significantly bias judgment of the geometric mean (Figures 4 and 5). With regard to ambiguous interval judgement, findings suggest that response bias alone does not have significant bearing on judgment of mean intervals, but rather that (a) a change in the distribution of probes *within-session* and (b) the number of probes prior to and following mean intervals may influence ambiguous interval categorization, as was observed in common probes test in Experiment 1 (Figure 3). That is, it is possible that there is a shift in responding as animals integrate feedback received from unreinforced probes within the session, leading to the shift in the psychophysical function which was observed between the skewed distributed probes and the within-session common probes test in Experiment 1 (Figures 1 and 3).

In order to further investigate this possibility, psychophysical functions were redrawn using only trials from the second half of last five session of distributed probes testing (Figure 9). The apparent reversal between the functions from all trials and that from only the trials in the second half of the sessions suggest that the observed “flip” in the functions between the distributed probes and common probes conditions could be attributed to a within-session shift in responding. Importantly, the apparent within-session shift in responding is most prominent in testing with large ratio skewed-short. probes (Figure 9d), as was observed in the common probes test in Experiment 1 (Figure 3). This pattern was also confirmed with simulations of the state-based interval timing model (Figure 10).

The state-based model of interval timing was also tested to account for results of the within-session common probes test. The primary procedural difference between the common probes test in Experiment 1 and judgment of the GM in Experiment 2 is that the common probes test was conducted in the second half of distributed probes testing sessions, as choices associated with those behavioral states which are similarly activated by both anchors and probes in close proximity to the anchors are strengthened. For example, the likelihood that an animal would choose “short” would increase over time with positively-skewed probes as “short” is strengthened for intervals close to the short anchor, such that the function would shift down. Simulations of a *full session* with common probes was conducted in order to show that ambiguous intervals can be influenced by within-session shifts in responding, similar to what was observed in distributed probes (Figure 8).

These simulations suggest that the observed pattern of results in the common probes test, in which animals judged ambiguous intervals as “short” more often following training with mostly short probes, can be accounted for by a within-session shift in responding, where the function for the trials from the second half of the session is shifted down compared to that from the whole session.

Limitations of the State-based Model of Interval Timing

Although it appears to account for many of the observed trends in the experimental data, the state-based model of interval timing presents a few notable limitations. In the experimental data with small anchor ratios, skewed probe distributions appear to make little difference on performance. In large anchor ratios, skewed-short distributions appear to shift the distribution leftwards. The state-based model reproduces this effect, as well as the within-session shift that pushes the response function of skewed-short probes rightward in the second half of the session. However, because simulations were conducted in “sessions” of 3000 trials, the model does not explain how this effect would reset between sessions, or why it is observed only in large anchor ratios. It is possible that this difference is because larger intervals activate a larger range of behavioral states, and thus, the activation of more disparate states by similar intervals enhances the observed effect.

Implications for Interval Timing Research

Results of the current study suggest that the effects of probe spacing in temporal bisection, which are omitted from many prominent theories of interval timing (Gibbon, 1977; Killeen & Fetterman, 1988), support a model of interval timing in which animals continue to time and modulate their judgment of intervals, even in the absence of

reinforcement. Further, it appears that the characterization of responses to probes as “samples” from an underlying psychophysical function is likely simplistic, and that the method of measurement in timing experiments should be carefully considered and interpreted, independent of an assumed underlying structure.

REFERENCES

- Akdoğan, B., & Balçı, F. (2016). The effects of payoff manipulations on temporal bisection performance. *Acta psychologica, 170*, 74-83.
- Allan, L. G. (2002). Are the referents remembered in temporal bisection? *Learning and Motivation, 33*(1), 10-31.
- Allan, L. G., & Gibbon, J. (1991). Human bisection at the geometric mean. *Learning and Motivation, 22*(1-2), 39-58.
- Araiba, S., & Brown, B. L. (2017). The effect of the long anchor duration on performance in the temporal bisection procedure. *Behavioural processes, 135*, 76-86.
- Brown, G. D., McCormack, T., Smith, M., & Stewart, N. (2005). Identification and bisection of temporal durations and tone frequencies: common models for temporal and nontemporal stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 31*(5), 919.
- Caselli, L., Iaboli, L., & Nichelli, P. (2009). Time estimation in mild Alzheimer's disease patients. *Behavioral and Brain Functions, 5*(1), 32.
- Church, R. M., & Deluty, M. Z. (1977). Bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behavior Processes, 3*(3), 216.
- Daniels, C. W., Fox, A. E., Kyonka, E. G., & Sanabria, F. (2015). Biasing temporal judgments in rats, pigeons, and humans. *International Journal of Comparative Psychology, 28*(1).
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological review, 84*(3), 279.
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of sciences, 423*(1), 52-77.
- Falter, C. M., Noreika, V., Wearden, J. H., & Bailey, A. J. (2012). More consistent, yet less sensitive: interval timing in autism spectrum disorders. *The Quarterly Journal of Experimental Psychology, 65*(11), 2093-2107.
- Fetterman, J. G., Killeen, P. R., & Evans, T. (1986). Timing and rate of reinforcement. *Unpublished data*.
- Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological review, 95*(2), 274.

- Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological review*, 104(2), 241.
- Machado, A., & Arantes, J. (2006). Further tests of the Scalar Expectancy Theory (SET) and the Learning-to-Time (LeT) model in a temporal bisection task. *Behavioural Processes*, 72(3), 195-206
- Machado, A., Malheiro, M. T., & Erlhagen, W. (2009). Learning to time: A perspective. *Journal of the experimental analysis of behavior*, 92(3), 423-458.
- Maia, S., & Machado, A. (2009). Representation of time intervals in a double bisection task: Relative or absolute? *Behavioural processes*, 81(2), 280-285.
- Machado, A., & Pata, P. (2005). Testing the scalar expectancy theory (SET) and the learning-to-time model (LeT) in a double bisection task. *Animal Learning & Behavior*, 33(1), 111-122.
- Parducci, A. (1963). Range-frequency compromise in judgment. *Psychological Monographs: General and Applied*, 77(2), 1.
- Parducci, A. (1965). Category judgment: a range-frequency model. *Psychological review*, 72(6), 407.
- Rakitin, B. C., Gibbon, J., Penney, T. B., Malapani, C., Hinton, S. C., & Meck, W. H. (1998). Scalar expectancy theory and peak-interval timing in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 24(1), 15.
- Raslear, T. G. (1983). A test of the Pfanzagl bisection model in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 9(1), 49.
- Raslear, T. G. (1985). Perceptual bias and response bias in temporal bisection. *Perception & Psychophysics*, 38(3), 261-268.
- Sanabria, F., & Killeen, P. R. (2008). Evidence for impulsivity in the Spontaneously Hypertensive Rat drawn from complementary response-withholding tasks. *Behavioral and Brain Functions*, 4(1), 7.
- Smith, A., Taylor, E., Warner Rogers, J., Newman, S., & Rubia, K. (2002). Evidence for a pure time perception deficit in children with ADHD. *Journal of Child Psychology and Psychiatry*, 43(4), 529-542
- Ward, R. D., Kellendonk, C., Kandel, E. R., & Balsam, P. D. (2012). Timing as a window on cognition in schizophrenia. *Neuropharmacology*, 62(3), 1175-1181.
- Watterson, E., Daniels, C. W., Watterson, L. R., Mazur, G. J., Brackney, R. J., Olive, M. F., & Sanabria, F. (2015). Nicotine-induced place conditioning and locomotor

activity in an adolescent animal model of attention deficit/hyperactivity disorder (ADHD). *Behavioural brain research*, 291, 184-188.

Wearden, J. H., & Ferrara, A. (1995). Stimulus spacing effects in temporal bisection by humans. *The Quarterly Journal of Experimental Psychology*, 48(4), 289-310.

APPENDIX A
EQUATIONS

(Eq 1.)

$$\text{Skewed - short. Probe } \{S, L, I, n\} = \frac{S [L (n - 1)]}{L (n - I) + S (I - 1)}$$

(Eq 2.)

$$\text{Skewed - long. Probe. } \{S, L, I, n\} = \frac{L + S - (L/S)^{(I-1)}}{S(n - 1)}$$

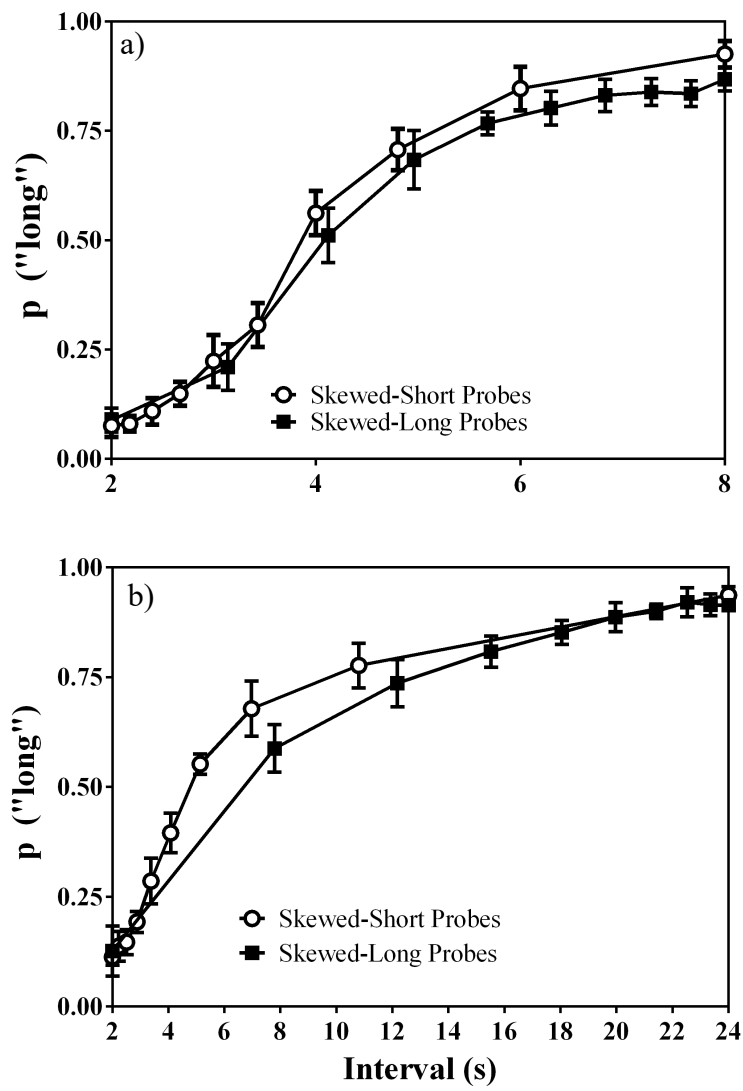
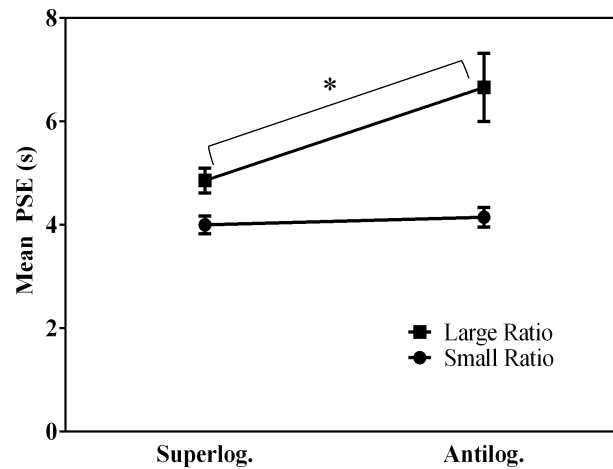


Figure 1. Psychophysical functions relating the probability of reporting “long” to the presented interval in the skewed-long and skewed-short distributed-probe conditions in the small anchor ratio condition (a) and in the large anchor ratio condition (b). This figure shows untransformed data. Error bars depict between-subjects SEM for the average p (“long”) for each interval in the last five sessions.



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Figure 2. Comparison of mean PSE (+/- SEM) obtained from skewed-long- and skewed-short distributed probe conditions. In the large anchor-ratio condition, but not the small anchor ratio condition, PSEs obtained from skewed-short distributed probes are smaller than those from skewed-long-distributed probes. *Strong evidence for the alternative hypothesis. Error bars depict between-subjects SEM of PSE (as calculated from psychophysical functions drawn from the last five days of each testing condition for each animal).

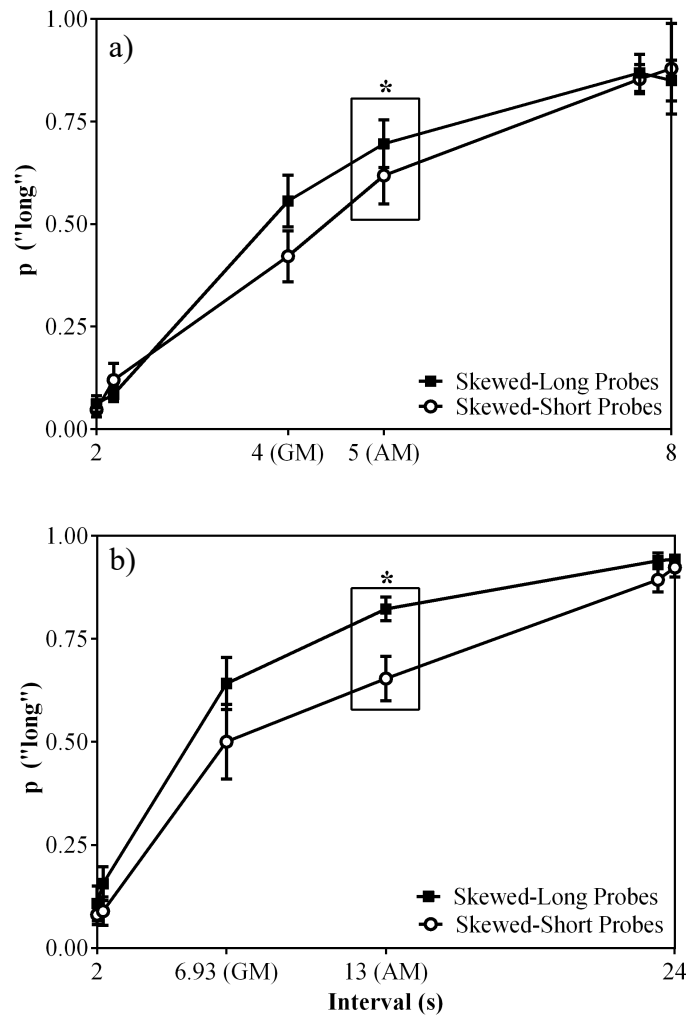


Figure 3. Psychophysical functions obtained from common probes following the skewed-long and skewed-short distributed probe conditions in the small anchor-ratio condition (a) and in the large anchor-ratio condition (b). In both ratio conditions, the arithmetic mean is judged as “long” more frequently in the skewed-long condition than in skewed-short condition. *Strong evidence at this interval for difference between distributed probe conditions. Error bars depict between-subjects SEM for the average p (“long”) for each interval.

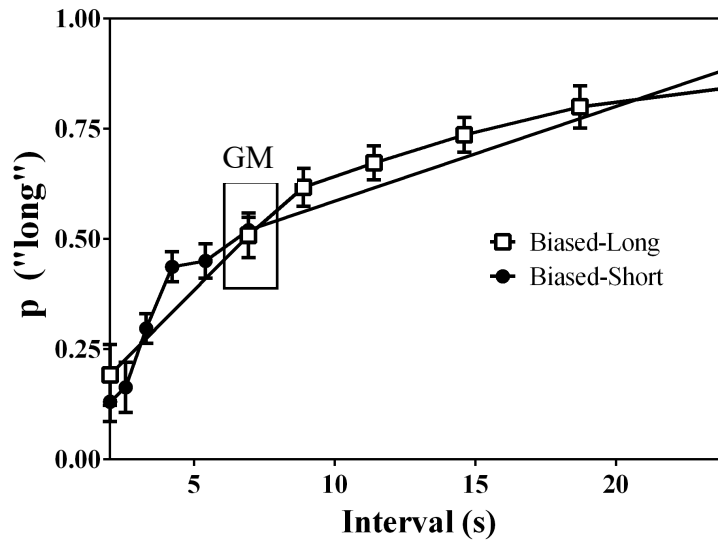


Figure 4. Psychophysical functions relating the probability of reporting “long” to the presented interval in the biased-long and biased-short probe conditions. There is no apparent shift in the psychophysical function between bias conditions, and inspection of p (“long” | GM) suggested no bearing of bias condition on judgement of the geometric mean. Error bars depict between-subjects SEM for the average p (“long”) for each interval in the last five sessions.

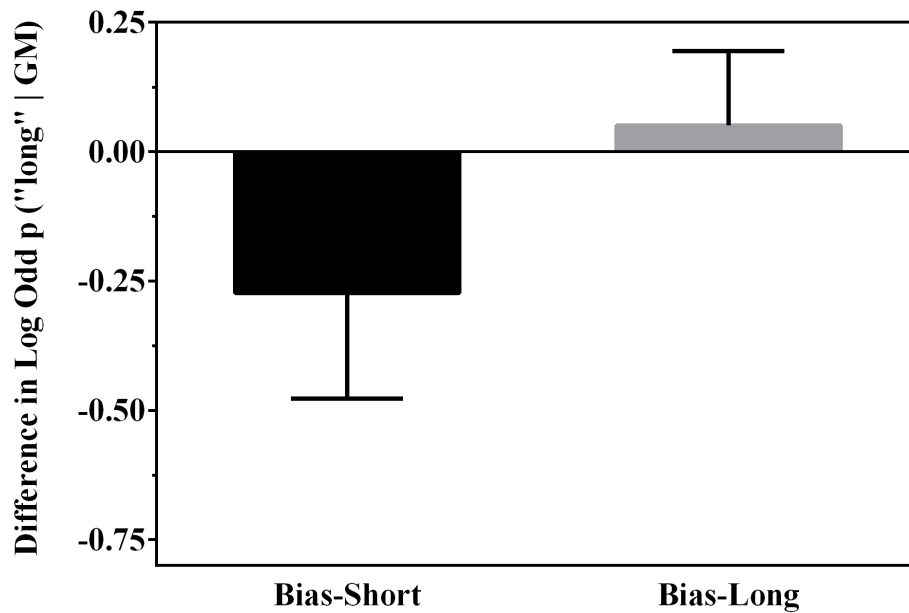


Figure 5. Difference in p (“long” | GM) from baseline in bias-short and bias-long conditions. Error bars depict between-subjects SEM for the average difference in log-odds from baseline of p (“long” | GM) in the last five sessions.

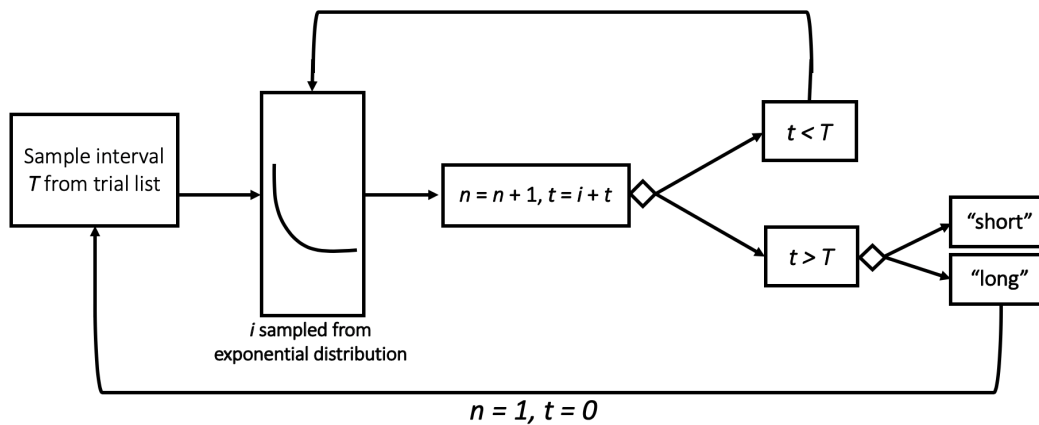


Figure 6. Schematic of state-based model of interval timing. The state-dwelling interval i is repeatedly sampled from an exponential distribution, and the state counter n is

incremented until $t > T$, at which point a choice (“short” or “long”) is made based on the probability of each choice given the active state at the end of the interval.

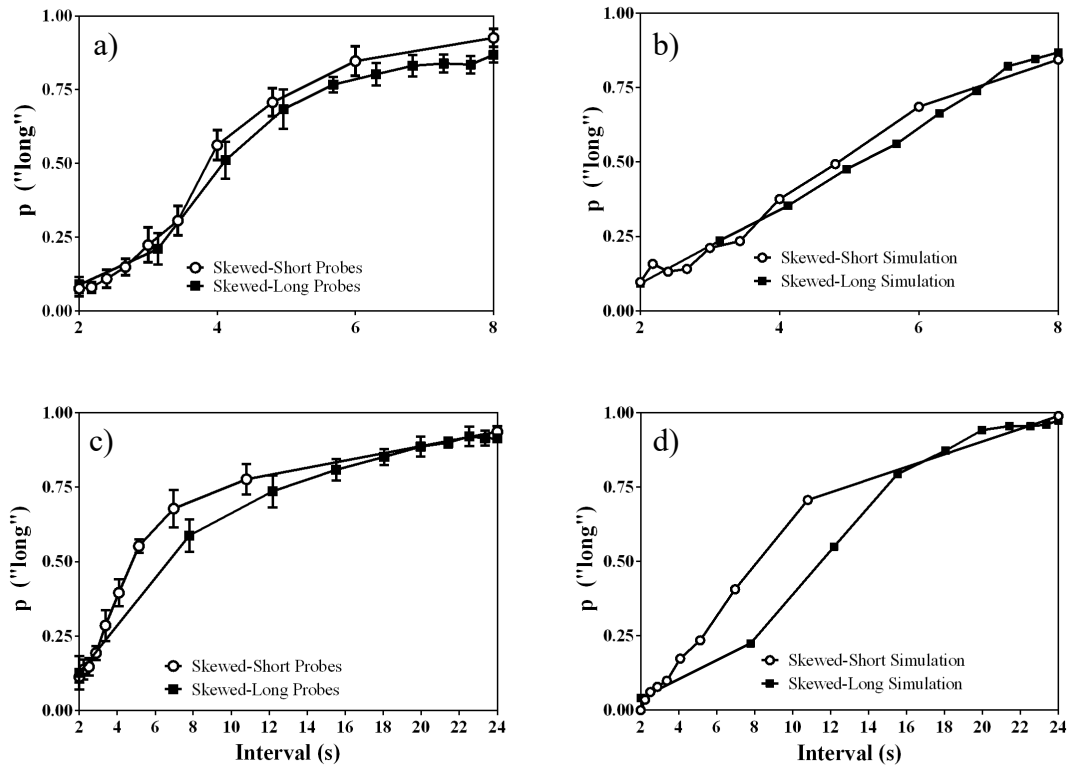


Figure 7. Experimental (a and c) and simulated (b and d) data using skewed-long and skewed-short probes in the small ratio (a and c) and large ratio conditions. In the large ratio condition, where the effect of skewed probes is enhanced, simulated data reflects the shift in psychophysical function observed in Experiment 1. Error bars in experimental data depict between-subjects SEM for the average p (“long”) for each interval in the last five sessions.

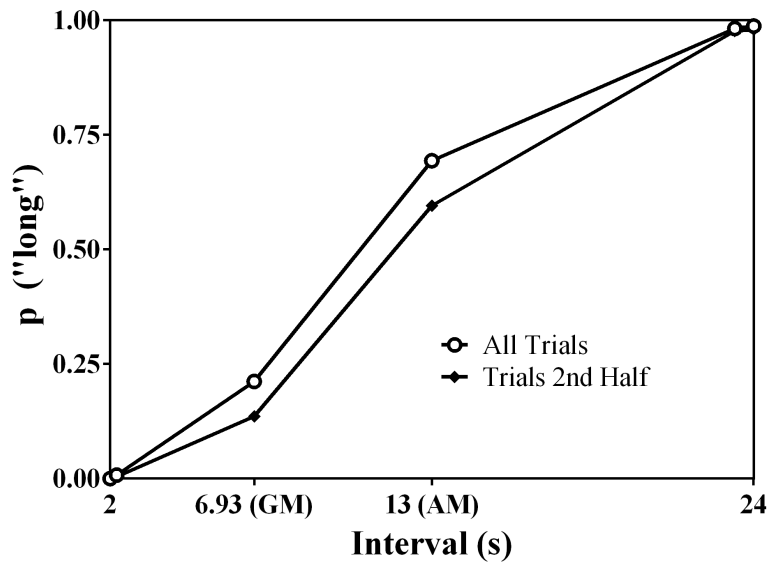


Figure 8. Simulated data for the common probes in the large ratio condition from Experiment 1, indicating that the state-based model of interval timing predicts of midsession shift in responding which could account for the observed “flip” in the psychophysical function between the distributed and within-session common probes observed in Experiment 1.

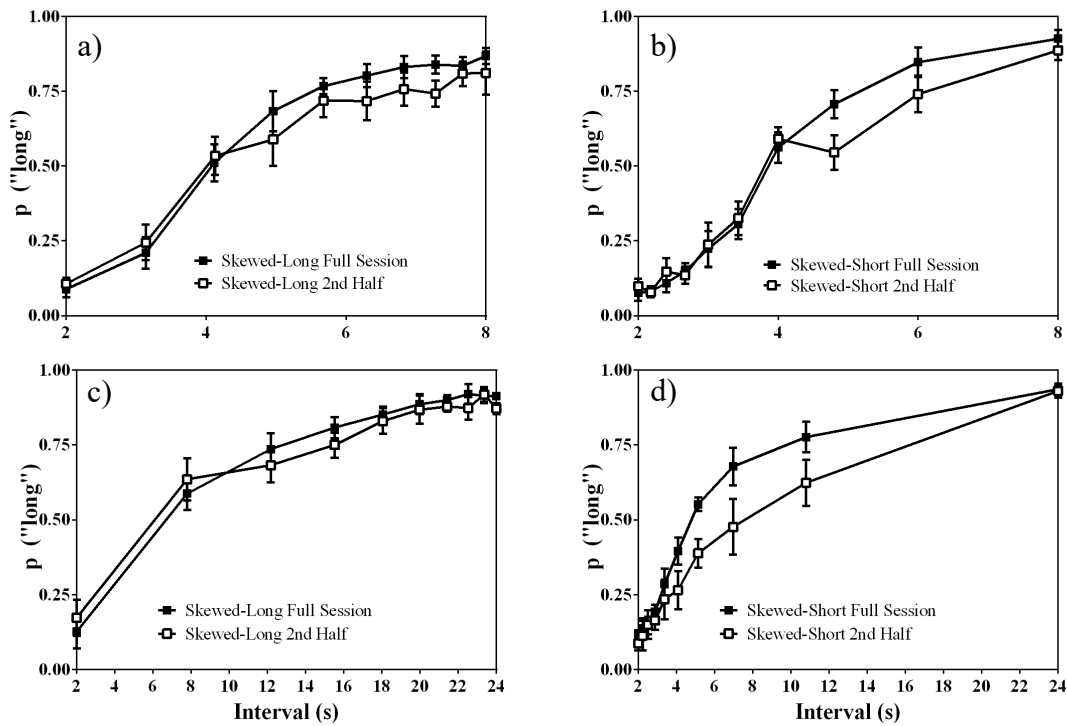


Figure 9. Psychophysical functions constructed from all trials in the last five sessions of distributed probes testing in Experiment 1 for the small (a and b) and large (c and d) anchor ratio conditions, compared to the functions constructed only from trials in the second half of the session. Functions indicate that, as animals integrate feedback from unreinforced probes within the temporal bisection session, responding shifts such that functions reverse, and responses elicited by active states which are associated with anchor are weakened. This is particularly salient in the skewed-short condition, similar to what was observed in the common probes test in Experiment 1 (Figures 1 and 3). Error bars in experimental data depict between-subjects SEM for the average p ("long") for each interval in the last five sessions.

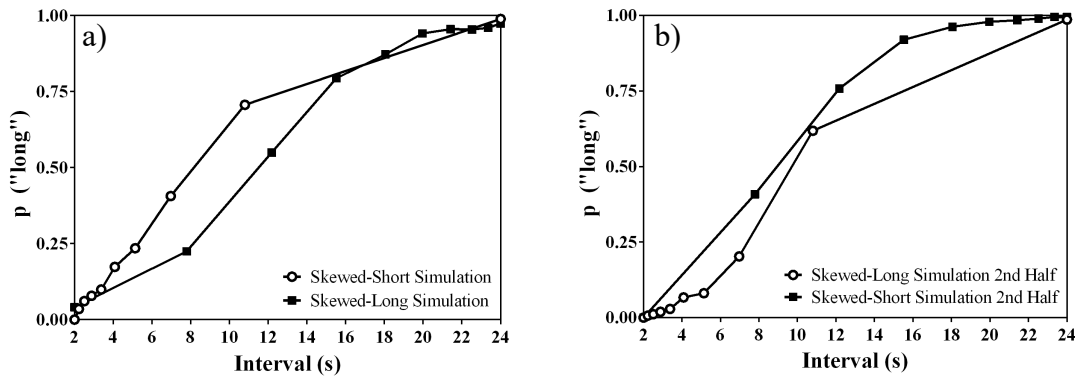


Figure 10. Psychophysical functions of simulated data for the large ratio condition constructed from (a) all trials within the session and (b) trials from only the second half of the session. Comparison to Figure 9 suggests that the state-based model of interval timing can account for the apparent within-session shift in temporal bisection responding observed when rats are tested with skewed probe distributions.

TABLES

Table 1. Experimental Design

Conditions	Group 1	Group 2	Group 3	Group 4
Anchor Training 1	Small Ratio	Small Ratio	Large Ratio	Large Ratio
Distributed Probes 1	Skewed-long	Skewed-short	Skewed-long	Skewed-short
Distributed Probes 2	Skewed-short	Skewed-long	Skewed-short	Skewed-long
Anchor Training 2	Large Ratio	Large Ratio	Small Ratio	Small Ratio
Distributed Probes 3	Skewed-long	Skewed-short	Skewed-long	Skewed-short
Distributed Probes 4	Skewed-short	Skewed-long	Skewed-short	Skewed-long

Note. Training and testing conditions are organized in chronological order, starting at the top.

Table 2. Anchor and distributed probe durations (in seconds)

Interval	Skewed-short Small Ratio	Skewed-short Large Ratio	Skewed-long Small Ratio	Skewed-long Large Ratio
Anchor	2.00	2.00	2.00	2.00
	2.18	2.23	3.14	7.79
	2.40	2.51	4.12	12.18
	2.67	2.88	4.96	15.52
	3.00	3.38	5.68	18.05
	3.43	4.08	6.30	19.97
	4.00	5.14	6.83	21.42
	4.80	6.97	7.28	22.53
	6.00	10.80	7.67	23.36
Anchor	8.00	24.00	8.00	24.00

Table 3. Anchor and common probe durations (in seconds)

Interval Type	Small-Ratio Intervals	Large-Ratio Intervals
Anchor	2.00	2.00
Minimum	2.18	2.23
Geometric Mean	4.00	6.93
Arithmetic Mean	5.00	13.00
Maximum	7.67	23.36
Anchor	8.00	24.00

Table 4. Descriptives and Bayesian t-tests for commons probes in small anchor-ratio condition

Interval (s)	Mean Log Odds p('long' Skewed-long)	Mean Log Odds p('long' Skewed-short)	SEM Skewed-long	SEM Skewed-short	$Log(BF_{10})$
2	-2.896	-3.141	.308	.290	-1.145
2.18	-2.691	-3.070	.297	.383	-1.004
4	0.223	-0.560	.242	.205	0.750
5	1.003	0.279	.249	.140	1.330*
7.67	1.554	1.460	.464	.438	-1.288
8	2.286	0.498	.386	.766	0.191

Table 5. Descriptives and Bayesian t-tests for commons probes in large anchor ratio condition

Interval (s)	Mean Log Odds p('long' Skewed-long)	Mean Log Odds p('long' Skewed-short)	SEM Skewed-long	SEM Skewed-short	$Log(BF_{10})$
2	-2.495	-2.805	.264	.239	-1.560
2.23	-2.219	-3.070	.284	.288	0.361
6.93	0.774	0.025	.216	.346	0.396
13	1.880	0.719	.218	.260	3.335*
23.36	3.087	2.972	.247	.292	-1.388
24	3.292	2.908	.189	.226	-1.193

Table 6. Experiment 2 Design

Conditions	Group 1	Group 2
Anchor Training	2-s vs. 24-s	2-s vs. 24-s
Baseline Probes 1	Geometrically-spaced	Geometrically-spaced
Biased Probes 1	Biased-short	Biased-long
Baseline Probes 2	Geometrically-spaced	Geometrically-spaced
Biased Probes 1	Biased-long	Biased-short

Note. Training and testing conditions are organized in chronological order, starting at the top.

Table 7. Anchor and probe durations (in seconds)

Interval	Baseline (Geometric)	Biased-Short	Biased-Long
Anchor	2.00	2.00	2.00
	2.56	2.56	-
	3.28	3.28	-
	4.21	4.21	-
	5.40	5.40	-
	Geometric Mean	6.93	6.93
	8.88	-	8.88
	11.38	-	11.38
	14.60	-	14.60
	18.72	-	18.72
Anchor	24.0	24.0	24.0