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BEHAVIOURAL
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Time left in the mouse

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Abstract

Evidence suggests that the online combination of non-verbal magnitudes (durations, numerosities) is central to learning in both human and non-human animals [Gallistel, C.R., 1990. The Organization of Learning. MIT Press, Cambridge, MA]. The molecular basis of these computations, however, is an open question at this point. The current study provides the first direct test of temporal subtraction in a species in which the genetic code is available. In two experiments, mice were run in an adaptation of Gibbon and Church's [Gibbon, J., Church, R.M., 1981. Time left: linear versus logarithmic subjective time. J. Exp. Anal. Behav. 7, 87–107] time left paradigm in order to characterize typical responding in this task. Both experiments suggest that mice engaged in online subtraction of temporal values, although the generalization of a learned response rule to novel stimulus values resulted in slightly less systematic responding. Potential explanations for this pattern of results are discussed.
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1. Introduction

Animals, both human and non-human, are extremely sensitive to statistical regularities in the world around them. A variety of species (rats, ducks, humans, and even fish) allocate the time spent at different foraging patches according to the relative rates of reinforcement at the two patches (e.g., Gallistel et al., in press; Godin and Keenleyside, 1984; Harper, 1982; Herrnstein, 1961; Leon and Gallistel, 1998)—a feat requiring not only the tracking of both the number of rewards delivered and the amount of time between each reward delivery, but also the computation of rate of reward (number/time; for review, see Gallistel, 1990). Similarly, human infants are sensitive to the frequency of co-occurrence of two syllable pairings, using complex implicit computations presumably to aide in the parsing of language (Aslin et al., 1999; Saffran et al., 1996). These phenomena and many others suggest that learning in a variety of domains involves the online, implicit computation of environmental statistics (Gallistel et al., 2005).

Despite the importance of these computations, very little is known about the non-verbal computation process, let alone about how they are instantiated biologically. A number of studies have directly tested the plausibility of non-verbal arithmetic in non-human animals and human infants and adults, all with great success. This series of investigations was initiated by the groundbreaking work of Gibbon and Church (1981) with the time left paradigm, aimed at clarifying the form of the mapping between objective and subjective magnitudes.

1.1. The original time left paradigm

Historically, there have been two main camps divided on this topic. One camp, following in the tradition of Fechner, argues that the relation between objective and subjective magnitudes is a logarithmic function, with the amount of noise in memory remaining constant, independent of size of the magnitude in memory (Dehaene, 1989; Dehaene et al., 1990; Reynvoet and Brysbaert, 1999). Thus, as values in memory get larger (e.g., memory for a long duration), these values are subjectively closer together, leading to more difficult discriminations. Alternatively, SET theory (Gibbon, 1977; Meck and Church, 1983) posits that subjective magnitudes are a linear function of objective magnitudes, with noise in memory increasing in direct proportion to the size of the magnitude in memory. Thus, the larger the value stored in memory, the more noise in the representation resulting in compromised discrimination abilities. Prior to the time left experiment (Gibbon and Church, 1981), data from timing

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and counting tasks were unable to tease apart these two claims since both predict the ubiquitous scalar variability observed in the behavioral data. That is, both accounts predict what has been observed time and again in the behavioral data—a proportional increase in response variability as a function of the mean value, such that the ease with which two values are discriminated is dependent upon their ratio in accordance with Weber's law (e.g., Brannon and Terrace, 2000; Cordes et al., 2001; Church et al., 1994; Rakitin et al., 1998).

In an attempt to clarify this debate, Gibbon and Church (1981) pitted predictions of these two theories against each other in a test of non-verbal subtraction. In two experiments, non-human animals were trained to press a lever/peck on a key (the comparison link) that would deliver a reward on a fixed interval schedule of, for example, 60 s. At some point in time, T, as the comparison interval was elapsing, a second lever/key option (the standard), that delivered food on a shorter fixed interval schedule (e.g., FI 30), became available to the animal. Thus, in order to maximize the number of rewards received, the animals needed to compare the standard duration (S) with the amount of time left on the comparison key ($C - T$). For example, if the standard option was made available 15 s into the trial, then responding on the standard lever would lead to reward following the standard interval (30 s). Responding on the comparison lever would lead to reward following the time left on that option ($C - T = 60 - 15 = 45$ s). So, a standard choice would lead to an earlier reward. Alternatively, if the standard was offered 45 s into the trial, the standard would again pay-off after the standard duration (30 s), but the latency on the comparison would only be ($C - T = 60 - 45 = 15$ s), making the comparison the better choice. Thus, early in the trial the standard option was the optimal choice and later in the trial, the "time left" option was.

The logic for this time left design was as follows: if there exists a linear relationship between subjective and objective time, behavioral responses would be a function of the arithmetic difference between the temporal intervals (the animals would respond as if comparing S with $C - T$). In this case, the animals would choose the standard early in the trial and the comparison later, with the point in the trial at which their preference switched varying as a function of $C - T$ (e.g., in the example above, the ideal switchover point would be at $C - T = 30$ s, although if the $C = 100$ and $S = 50$, then the switchover point would move to $C - T = 50$ s). On the other hand, if logarithmic compression is involved, the subtraction of mental magnitudes would involve the subtraction of logarithms, mathematically translating into the ratio of the two values [because $\log X - \log Y = \log(X/Y)$]. In this case, responding was predicted to be a function of the ratio of the two temporal intervals and independent of their arithmetic difference. According to this model, the subjective arithmetic difference between 60 and 30 should be equivalent to that between 100 and 50. Although rather counter-intuitive, this model predicted that the point at which the animal's preference changes (known as the point of subjective equality or PSE) would vary with the ratio of the comparison to standard interval. Thus, the PSE in a $C = 60$, $S = 30$ s situation should be identical to that in a $C = 100$, $S = 50$ s condition.

Gibbon and Church tested both rats and pigeons varying the temporal parameters of the comparison and standard FIs, keeping the ratio between the two values held constant at 2:1. Data analyses indicated that the animals responded as a function of the arithmetic difference between the two temporal values, not of their ratio—thus supporting Gibbon and colleagues' claims of a linear mapping between objective and subjective magnitudes, as well as providing the first direct evidence of arithmetic capabilities in non-human animals.

Since the original time left experiment, this paradigm has been adopted for use with adult humans (Wearden, 2002) and to include numerical stimuli in a number left analogue (Brannon et al., 2001) and results of these studies continue to support a linear mapping as proposed by SET. Although results are robust, there has been debate about the conclusions drawn. Dehaene (2001) has suggested that the assumption of a logarithmic mapping can be salvaged by assuming that subtraction is implemented by table-look-up. When the results of combinatorial operations are found by table-look-up, there are no constraints on the relation between the operands and the looked up results. Thus, the value for the difference of two subjective magnitudes need not be their actual difference; it can be the logarithm of the difference of their antilogs (that is, the logarithm of the difference between the two values of real time rather than the difference in the logarithms of those values).

Table-look-up using logarithmic values is problematic for subtraction, because differences may be positive, 0 or negative. The logarithm goes to negative infinity at 0 and (real-valued) logarithms for negative differences do not exist, so one would expect to see something unusual when the results of non-verbal mental subtraction are equal to or less than 0. However, recent data on the variability in the signed answers to non-verbal mental subtraction problems show the same variability at and around 0 difference as is observed when the answers are positive and well away from 0 (Cordes et al., 2006). Also, table-look-up models for combinatorial arithmetic operations appear to require the positing of a separate table for each pair of variables to be combined, and, within each such table, a separate cell (neural circuit) for every pair of values whose difference (or sum, or product or quotient) is to be found (Gallistel, in press; Gallistel et al., 2001). This makes them unattractive models for something as basic and (we assume) ubiquitous as arithmetic combination.

Others (Cerutti and Staddon, 2004; Preston, 1994; Staddon and Higa, 1999) have suggested models in which elapsed time is measured by a decay process and prospective intervals (time left and the standard time) are measured by an immediacy, which is the reciprocal of the prospective interval. Decay models of interval timing appear unable to explain scalar variability, which is observed in the time left task as in other timing tasks (Gallistel, 1999). In addition, findings from a wide variety of subsequent paradigms testing non-verbal arithmetic in both human and non-human species (e.g., Barth et al., 2006; Boysen and Berntson, 1989; Brannon et al., 2001; Cordes et al., 2006; McCrink and Wynn, 2004; Rumbaugh et al., 1987; Wearden, 2002; Wynn, 1992) have further supported Gibbon and Church's original claims that the time left results indicate that subjective mag-

nitudes, and their corresponding subjective noise, are directly proportional to the objective magnitudes they represent.

1.2. The current study

Although non-verbal computations have been implicated as a crucial component in learning, there is still very little known about the computational process. Studies such as the time left paradigm have opened the door for tests of explicit non-verbal arithmetic in both human and non-human species. How the computational process is instantiated at the molecular level is unknown, however. One way to begin such a biological investigation is to design behavioral screens that identify animals impaired in this ability, possibly leading to the identification of the genetic components of this impairment (Gallistel et al., 2004). But to do this, we must first begin with a species in which the molecular substrate is available. In this paper, we describe an adaptation of a test of explicit arithmetic – the time left paradigm (Experiment 1) – to a novel species, the mouse. In the spirit of the work of Gibbon and Church, we perform a detailed quantitative analysis of timing behavior in these animals in order to provide a characterization of typical mouse performance in the time left task.

2. Experiment 1

2.1. Materials and methods

2.1.1. Subjects

The subjects were six naïve female Swiss-Webster ND4 mice. Subjects were individually housed and kept on a 12:12 h light:dark schedule with lights on at 08:00 h. All training took place during the dark portion of their light schedule. Mice were maintained at approximately 90% of their free-feeding weight. Water was available *ad lib*.

2.1.2. Apparatus

Mice were run in Med-Associates operant chambers that were kept in sound attenuating boxes. Each chamber had four hoppers equipped with infrared beams to detect entries and lights that could be turned on to illuminate the hopper. One hopper (the control hopper) was on the opposite side of the chamber as the other three. Only the control hopper and the two side hoppers (termed the comparison and standard hoppers) were used in this experiment (the center hole was not used). The two side hoppers were connected to a feeder that delivered one .02 g pellet per feeding. The chambers were also equipped with white noise and tone generators. Water bottles were filled and available throughout the session. Operant chambers were controlled by a Med-Associates interface, and experiments were programmed in MedPC code.

2.1.3. Procedure

There was no initial training phase of the experiment—the naïve mice were first exposed to the following design. Following a variable inter-trial interval $(90\,s + E(5\,s))$, the light came on in the control hopper signaling that the trial could be initiated. All trials were mouse initiated; thus the mouse had to poke its head into the illuminated control hopper, breaking the infrared beam, in order to initiate the trial. Once the trial was initiated, the light in the control hopper extinguished and the white noise turned on, signaling the beginning of the comparison FI (C). At a random time T during the comparison FI (chosen uniformly anywhere from 1 to $C - 1$ s), the white noise was turned off (indicating that the comparison FI was no longer elapsing) and the mouse was expected to make a response. There were two different kinds of trials.

2.1.3.1. Choice trials (80% of all trials). On choice trials, at time T when the white noise turned off, the mouse was given a choice between the amount of time left on the comparison hopper ($C - T$) and the standard FI (S). That is, the lights in both the comparison and standard hopper illuminated at time T, and the first nose poke into either hopper activated that hopper, and the mouse was fed following the latency associated with that hopper. If the mouse broke the infrared beam in the comparison hopper, the white noise would turn back on and a pellet would be delivered following the time left associated with that hole ($C - T$). If, on the other hand, the mouse poked its head into the standard hopper, the tone was turned on (signaling the standard FI) and a pellet was delivered following S.

2.1.3.2. Forced trials (20% of all trials). On forced trials, at time, T, when the white noise was extinguished, the mouse was not given a choice between both hoppers, but was forced to initiate the FI associated with one of the holes. That is, on half of these trials, only the light in the comparison hopper turned on, and once the mouse stuck its head in this hole, the white noise turned back on and a pellet was delivered following the time left associated with that hole. On the other half of these trials, only the standard hopper light was illuminated, and once the mouse poked its head in that hole, the tone would turn on and the animal was rewarded following the latency associated with the standard hopper. These trials were included in order to teach and reinforce the latencies associated with both holes.

Sessions lasted 2 h. There were two phases to the experiment. In the first phase (69 sessions), all mice were trained with a comparison FI of 40 s and a standard FI of 20 s. In the second phase (28 sessions), half of the mice (#181–183) were switched to $C = 20$ s and $S = 10$ s (keeping the comparison/standard ratio constant at 2:1, as in Gibbon and Church, 1981), and the other three mice (#184–186) were switched to $C = 80$ s and $S = 40$ s.

2.2. Results and discussion

All analyses were performed on data from choice trials from the last 15 sessions of each experimental phase. Trials in which the mouse took longer than 6 s to poke its head in one of the holes (after the choice was offered at T) and those in which the mouse already had its head in the hole in anticipation of feeding were excluded from analyses.

Plots of the cumulative number of trials in which the mouse chose the comparison hopper as a function of when the choice was offered (T) in the first experimental phase are shown in Fig. 1
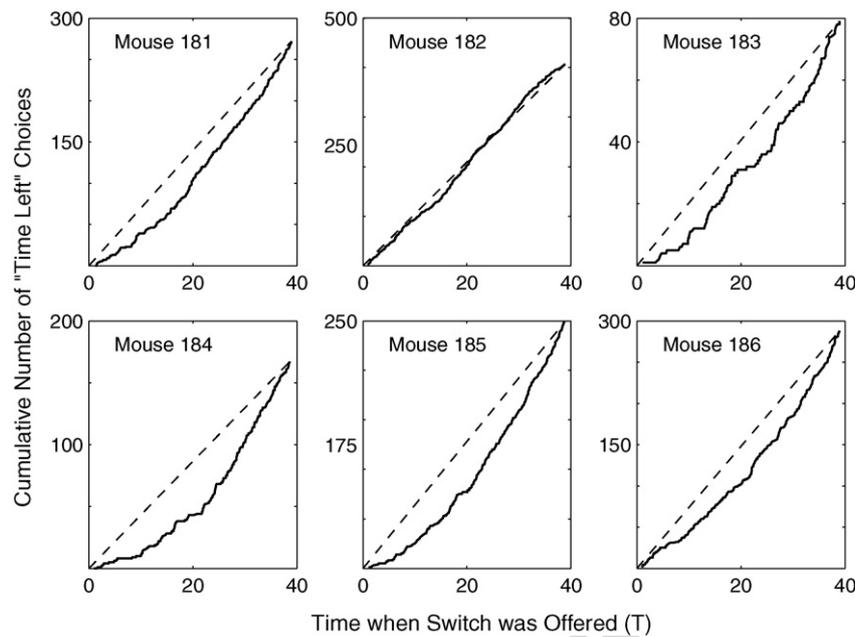
Fig. 1. The cumulative number of comparison hopper choices as a function of time when the choice was offered (*T*) for the first experimental phase of Experiment 1 (solid lines). The dashed lines indicate what performance would look like if responding did not vary as a function of the time left on the comparison hopper.
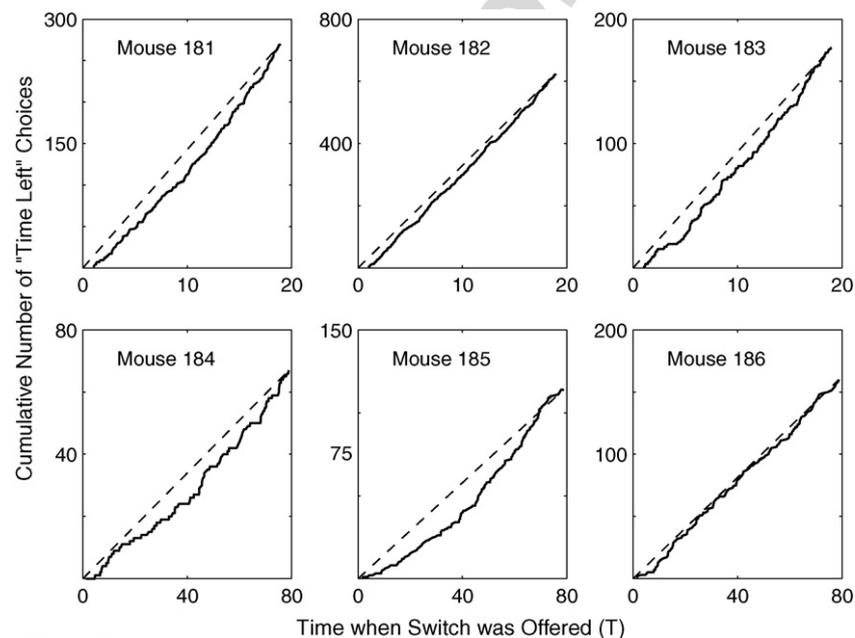
Fig. 2. The cumulative number of comparison hopper choices as a function of time when the choice was offered (*T*) for the second experimental phase of Experiment 1 (solid lines). The dashed lines indicate what performance would look like if responding did not vary as a function of the time left on the comparison hopper.

(solid line). If responding did not vary as a function of the time left on the comparison hopper, these plots would yield straight lines (as denoted by the dashed lines in Fig. 1). Ideal responding however, that is, responding dependent upon the time left on the comparison hopper, would reveal a very shallow slope for times early in the trial (since choosing the comparison early in the trial leads to a longer latency to reward), with a dramatic increase in slope starting at or near the middle of the trial. In this case, the cumulative plots would fall below the straight lines. As can be seen from these plots, this was the case for five of

the six mice.[1] In these plots, the cumulative curves fall below the straight line, revealing a shallower slope in the beginning of the trial followed by an increase in the probability to choose

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[1] Mouse 182 produced approximately linear data in this cumulative measure, although this is attributed to this animal's large bias for the comparison hopper. As can be seen from sigmoidal fits of the data (Fig. 4), despite this bias, the animal's tendency to choose the comparison did vary systematically as a function of the time left.
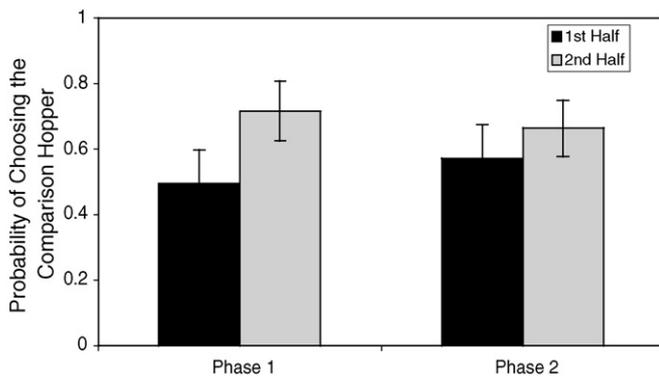
Fig. 3. Average probability of a comparison hopper choice for when the choice was offered in the first half vs. the second half of a trial for both experimental phases in Experiment 1.

the time left key for greater values of *T*. This trend was also apparent (although slightly less robust) in the data from the second experimental phase, in which the mice adjusted to novel temporal values (Fig. 2).

The pattern of results observed in these plots was confirmed by determining the probability of a time left choice when the choice was offered in the first half of the trial versus the second half. For example, when looking at data from the first experimental phase, we examined the probability of the mouse choosing the comparison hopper when the choice was offered in the first 20 s of the trial as compared with the probability associated with choices offered in the last 20 s of the trial. All six mice revealed an increased preference for the time left on the comparison hopper when the choice was offered later in the trial in both experimental phases (binomial, $p < .05$), and the differences in the average preference was reliable in both phases

(repeated measures *t*-tests—Phase 1: $t(5) = 4.13$, $p < .01$; Phase 2: $t(5) = 4.70$, $p < .01$—see Fig. 3).

Results reveal a clear tendency for the mice to prefer the comparison hopper once the remaining latency on the comparison hopper was less than that of the standard across both experimental phases. Further analyses, however, suggest that responding in the second experimental phase was much less orderly and systematic than with the initial experimental values. This result is apparent when the data are fit with sigmoidal functions in order to determine the point during the session at which the mouse revealed a (relative) indifference between the time left on the comparison hopper and the standard hopper (point of subjective equality, or PSE, as denoted by the point on the curve corresponding to .5 probability of picking either hopper). To do so, the data were divided into six equally spaced bins as a function of trial time, and response biases were eliminated by subtracting out the minimum probability of choosing the comparison hopper and dividing by the range of probabilities ($y' = (y - min)/(max - min)$). This transformation equates the lowest probability to a zero probability, and the maximum probability to one (see Table 1 for the untransformed minimum and maximum probabilities of choosing the comparison hopper, as well as for the PSEs returned by these fits, for each mouse and each experimental phase).

When this analysis is performed on the data from Phase 1 (Fig. 4), the data reveal a clear pattern of responding, and the data are well fit by sigmoidal functions, revealing PSE's near 20 s (the point of optimal responding in this task—see Table 1). These results suggest that the mice engaged in online subtraction to make the $C - T$ versus S comparison in order to minimize the latency to reward. The data from Phase 2, however, are not nearly as systematic. Unfortunately, sigmoidal functions do not
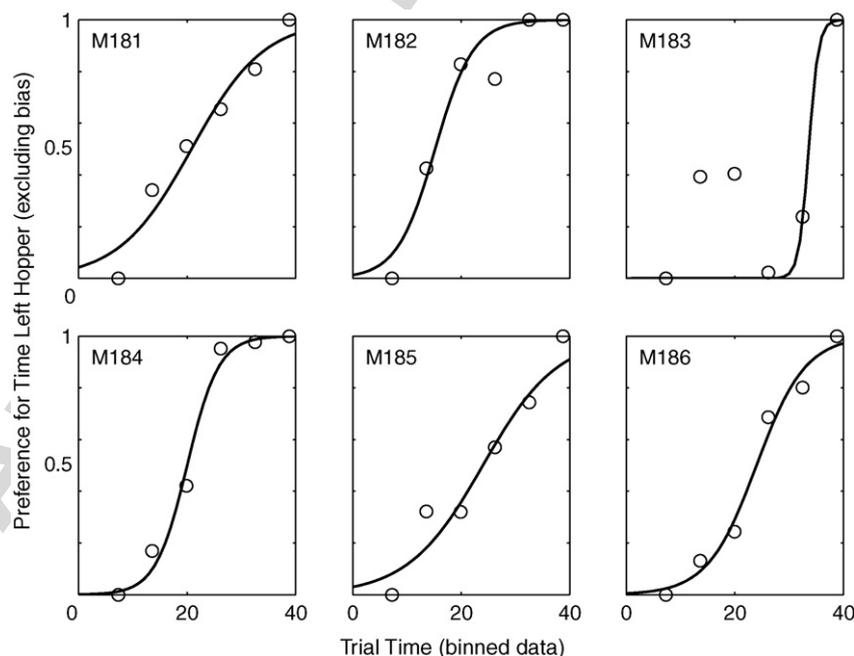
Fig. 4. Preference for the comparison hopper as a function of trial time with their corresponding maximum likelihood sigmoidal fits for the first experimental phase. The plotted points are obtained by dividing the data into six equally spaced bins and eliminating bias by subtracting the minimum probability and dividing by the range.
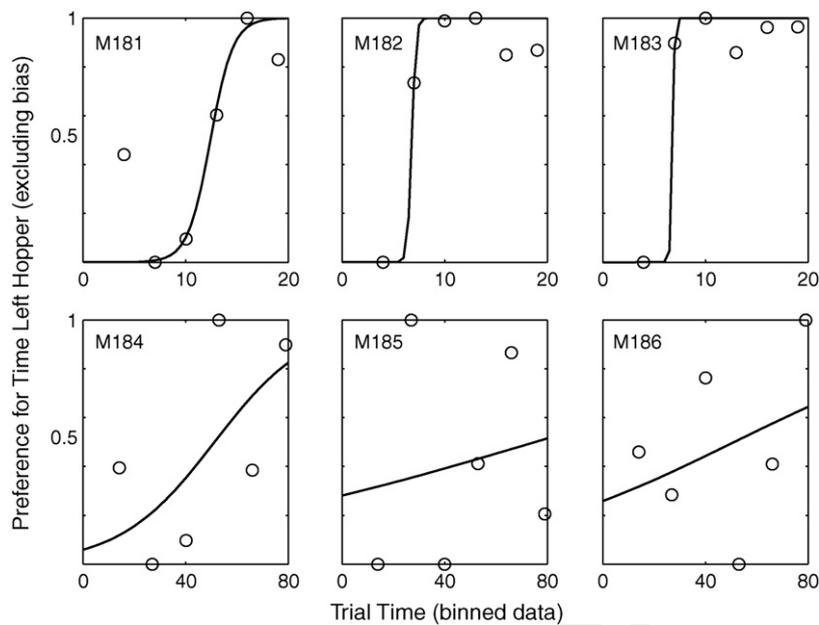
Fig. 5. Preference for the comparison hopper as a function of trial time with their corresponding maximum likelihood sigmoidal fits for the second experimental phase.

adequately characterize the data from most of the mice from this phase (Fig. 5), limiting the validity of the PSE measure.

Results of Experiment 1 suggest that mice are able to keep track of the amount of elapsing time and compare it to a standard interval, most likely via some form of online subtraction. Although this overall pattern of results was observed across two different temporal pairings (i.e., both experimental phases), analyses reveal that systematicity in responding deteriorated in the second experimental phase. There are a number of possibilities for this result. It is possible that the mice in this experiment were over-trained in the first experimental phase (69 sessions), and thus an adjustment to novel values may have been too difficult a task for the animals. In turn, it is possible that the animals were under-trained in the second experimental phase (28 sessions). It may also be the case that the adjustment to two

novel temporal values (both the comparison and the standard FIs were switched in the second experimental phase) may have led to impaired performance due to excessive cognitive demands. Some of these possibilities were evaluated in a second experiment.

3. Experiment 2

In Experiment 2, we tested a slightly different adaptation of the time left procedure to six new mice. In this paradigm, the animals were expected to make an online decision regarding whether or not to choose the standard hopper (i.e., the comparison latency continued to elapse once a choice was offered). Experimental phases differed only in the value of the standard latency (the comparison latency remained at 40 s throughout the experiment). In addition, the first experimental phase lasted for half as many sessions as in Experiment 1, and the second experimental phase involved slightly more experimental sessions to account for an imbalance in experience with temporal values. This experiment also included a third experimental phase in which the standard value was changed a third time, allowing us to counterbalance the order of presentation of the three standard values across subjects.

3.1. Materials and methods

3.1.1. Subjects

Six naïve female c57 bl/6 mice[2] were run in this experiment. Animals were maintained at approximately 90% of their free-feeding weight. All animals were housed individually, and the

Table 1

Untransformed minimum and maximum probabilities of choosing the time left on the comparison hopper, and the PSEs returned by sigmoid fits of the data for Experiment 1

	Minimum probability	Maximum probability	PSE
Phase 1			
M181	.34	.87	20.4
M182	.91	1.00	15.2
M183	.25	.66	33.6
M184	.13	.54	20.4
M185	.37	.94	23.6
M186	.37	.85	24
Phase 2			
M181	.55	.77	12.6
M182	.85	.99	6.6
M183	.22	.42	6.8
M184	.20	.48	51.2
M185	.58	.79	74.4
M186	.67	.87	50.4

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[2] We switched to using c57 bl/6 mice in this experiment because this strain of mouse is commonly used as the background strain in genetic studies, and thus more likely to be used in behavioral screens in the future.

experiment was run at approximately the same time everyday during their dark cycle.

3.1.2. Apparatus

The apparatus was identical to that of Experiment 1.

3.1.3. Procedure

Trials were again mouse initiated. Following a variable inter-trial interval ($E(60 s)$), the light on in the control hole illuminated. Once the mouse poked its head in this hole (breaking the infrared beam), the control hole light turned off, and the trial began. Again, there were two kinds of trials.

3.1.3.1. FI trials (1/3 of all trials). These trials were incorporated to ensure the animals learned the fixed intervals associated with each hole. On these trials, either the comparison *or* the standard hopper was illuminated, signaling the latency associated with that hole was elapsing. Once the fixed interval elapsed, a pellet was delivered, independent of the animal's behavior.

3.1.3.2. Choice trials (2/3 of all trials). On these trials, the comparison hole was illuminated first, signaling the FI associated with that hole (40 s) began to elapse. At one of six possible times, T, into the interval ($T = 0, 6.25, 10, 15, 22.5$ or 33.75 s—the order of presentation of these times was randomly determined by the computer), the standard option was offered, signaled by a blinking light in the standard hopper. If the mouse poked its head in the standard hole, the comparison hole light was turned off and a pellet was delivered in the standard hole after the standard latency. If the mouse did not poke its head in the standard

Table 2
Experiment 2

Standard FI	Phase 1 (34 sessions) (s)	Phase 2 (39 sessions) (s)	Phase 3 (15 sessions) (s)
Mice 161–163	20	10	30
Mice 164–166	20	30	10

hole, then a pellet was delivered in the comparison hopper once the comparison interval elapsed, independent of the mouse's behavior.

Throughout the experiment, the comparison latency was set at FI 40 s. The standard latency, however, varied as a function of experimental phase (see Table 2). In the first phase (34 sessions), the standard latency was FI 20 s for all mice. In the second experimental phase (39 sessions), half the mice were switched to a standard FI 10 s and the other half had a standard FI 30 s. In Phase 3 (15 sessions), these contingencies were reversed (i.e., FI 30 and FI 10 s for each group of mice, respectively).

3.2. Results and discussion

Data collected from choice trials during the last 10 days of each phase were analyzed. The probability of each animal staying with the time left on the comparison hopper is plotted as a function of the time the standard choice was offered during the trial for each standard FI is plotted in Fig. 6. Through these data points are the best fitting linear regressions of the data. All of these regressions had significantly positive slopes (one-tailed t-tests, $p < .05$), suggesting that the probability of not choosing the standard (and thus staying with the time left on the comparison
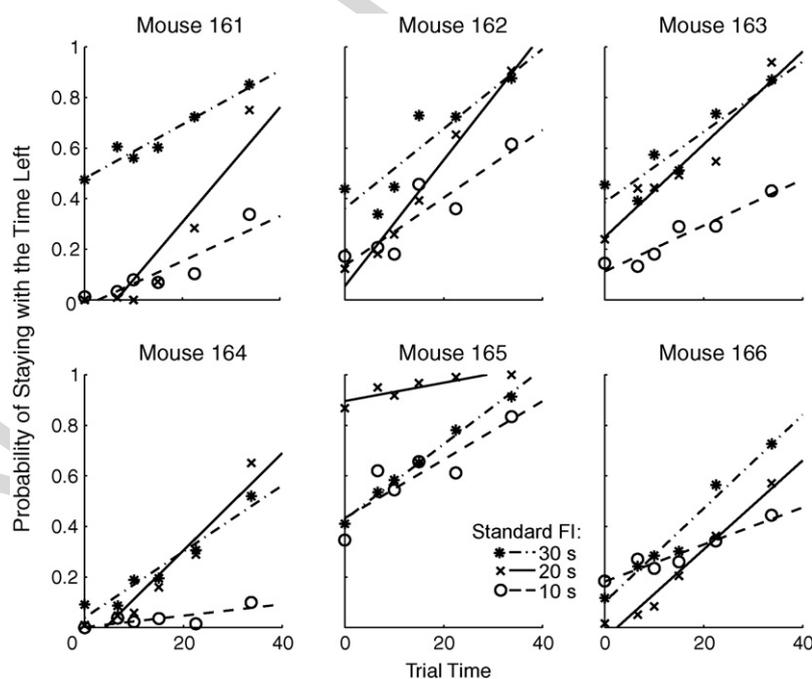
Fig. 6. Probability of not taking the standard option (and thus, staying with the time left on the comparison hopper) as a function of when the switch was offered during the trial (T) for each phase of Experiment 2. Empty circles: standard = 10 s, ×'s: standard = 20 s, and filled circles: standard = 30 s. Lines through the data points denote linear regressions of the data.
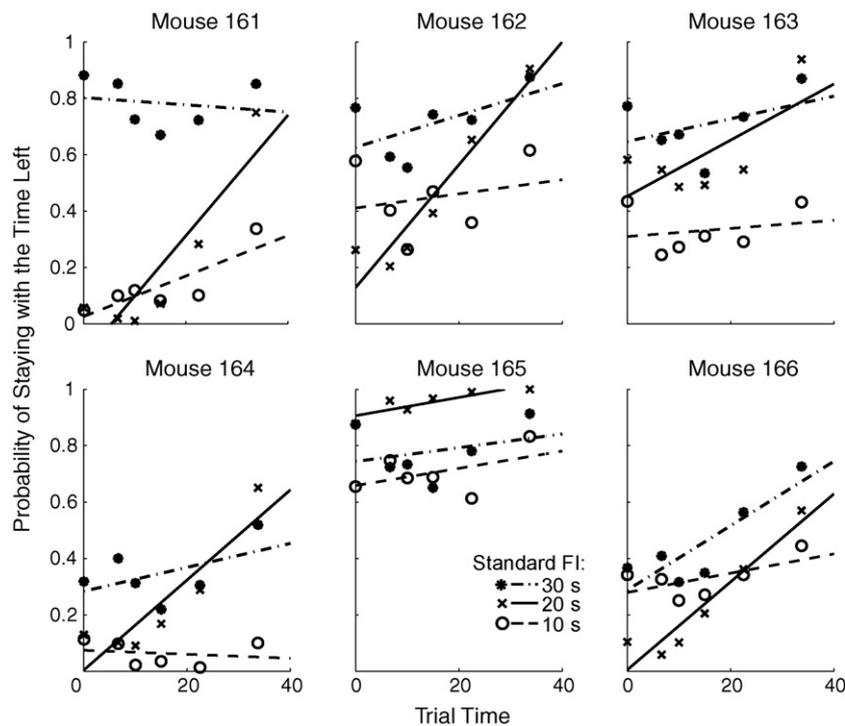
Fig. 7. Probability of not taking the standard option (and thus, staying with the time left on the comparison hopper) within the first 6.25 s of when the standard option was offered (*T*) as a function of *T* for each phase of Experiment 2. Empty circles: standard = 10 s, ×'s: standard = 20 s, and filled circles: standard = 30 s. Lines through the data points denote linear regressions of the data.

hopper) increased as the amount of time left on the comparison hopper decreased.

Unfortunately, this initial look at the raw data may present a biased picture of responding. This is because the earlier the standard option was offered during the trial, the longer the animal had to choose the standard option. For example, if the standard hopper began to flash immediately (0 s into the trial), then the animal had a full 40 s to switch to the standard option. In contrast, when the standard option was offered 33.75 s into the trial, there was only a 6.25 s window during which a switch could be made. This bias in the experimental design led to follow-up analyses of the raw data. To account for this bias, the data were reanalyzed by looking at the probability of the animal not picking the standard option (and thus staying with the time left on the comparison hopper) within the first 6.25 s after the standard option was offered. These values and the best fitting linear regressions are plotted as a function of trial time in Fig. 7.

From these plots, it is evident that the pattern found in the initial (biased) analyses holds for the data from the first experimental phase (denoted by ×'s and the solid line in Fig. 7). That is, when the standard was 20 s, all six animals varied their responding as a function of the amount of time left on the comparison hopper—they were more likely to switch to the standard hopper early on in the trial than later, revealing they were able to keep track of the amount of time left on the comparison hopper. This was again confirmed by one-tailed *t*-tests of the data from each individual mouse (*p* < .05 for all mice, except the data from mouse 163 approached significance, *t*(4) = 1.98, *p* = .059). This pattern of results held for the second phase of the experiment, with all linear regressions yielding positive slopes relating the

probability of staying with the time left as a function of *T*. In the third phase, four of the six mice revealed a decreased tendency to choose the standard as a function of the time left on the comparison hopper. Interestingly, despite the fact that training in the second phase was longer than in the first phase of the experiment, results were much noisier, with only 2 of these regressions (from mice 161 and 166) yielding significant slopes. None of the slopes in the third phase reached significance (*p* > .05).

Thus, results suggest that the mice were able to respond as a function of the time left on the comparison hopper. This contingency held when the standard duration was changed, although responding was less consistent and systematic. This result mirrored that of Experiment 1, despite less training in the first phase and more training in the second phase, and despite the fact that only one FI was changed across phases. Interestingly, in this experiment, the duration of the standard also had an effect on overall responding. This is evidenced in looking at the overall probability of the animal choosing the standard option (independent of trial time or time the standard option was made available). This statistic was inversely correlated with the standard duration, such that shorter standard FI elicited a greater number of switches (Fig. 8). This inverse relationship between the probability of choosing the standard and the standard FI value was found in all six mice, and a *t*-test revealed that the obtained regression slopes were significantly different from zero (*t*(5) = 2.96, *p* < .05). This was not the case with responding in Experiment 1, in which the probability of choosing the comparison hopper did not vary as a function of experimental phase (*t*(5) = .320, *p* > .05). Although variations in experimental design may be able to account for this difference, this novel result may also indicate
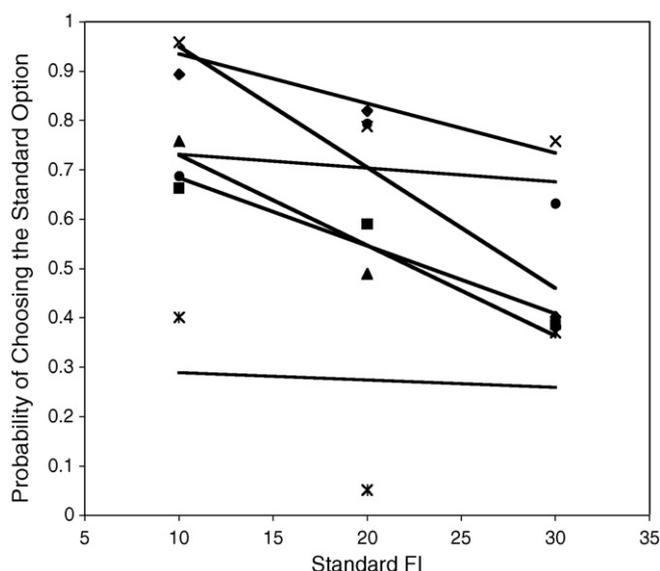
Fig. 8. Overall probability of choosing the standard as a function of the standard FI for all six mice in Experiment 2. Lines denote linear regressions of the data for each mouse.

that the absolute difference between the comparison and standard latencies, and not the ratio (which was held constant in Experiment 1), may have influenced the mouse's overall preference for the time left on the comparison hopper.

4. Discussion

The experiments described above serve as the first direct test of temporal subtraction in the mouse, a species in which the genetic code has been determined. Thus, they provide the first window into examining the molecular foundations of non-verbal computations, processes implicated in learning in a vast array of domains in both human and non-human animals.

Our results suggest that mice were able to keep track of the amount of time that has elapsed $(C - T)$ and compare it to a fixed standard interval (S), a task involving the computation of the difference between two temporal values. This finding was most apparent in the first phase of both experiments, in which the mice were initially trained in the task and had experience with only one pair of temporal values. All mice responded as a direct function of the time left on the comparison hopper, with the probability of initiating the standard link decreasing with the amount of time left, suggesting that the mice engaged in temporal subtraction. Thus, importantly, our findings replicate and expand the Gibbon and Church (1981) time left findings to a novel species, opening the door for future behavioral genetics investigations of non-verbal computations.

Results of our study also highlight important across- and within-species distinctions. While all mice responded as a clear function of the time left in the initial experimental phase, when the fixed interval values were changed, despite extensive experience with these novel values, not all mice were able to adjust their behavior accordingly. Although most mice continued to respond as a function of the time left on the comparison hopper, simply modifying their overall preference for the standard hop-

per, some mice failed to generalize the temporal contingency to the novel intervals. This pattern of results was evident in both experiments—when both values were changed or just the standard value, and when the initial training experience was extensive (69 sessions) or comparable to that of Gibbon and Church.

Thus, while all mice learned to base their behavior upon the difference of two temporal values, not all generalized this response rule to novel values. There are a number of non-mutually exclusive explanations for this finding. It could be that the animals were over-trained in the first phase of the experiment, although the number of training sessions in Experiment 2 (34 sessions) is fairly comparable to that of the second experiment of Gibbon and Church (28 sessions, although it should be noted that this experiment was performed with pigeons). It may also be the case that the animals were under-trained in the second phase of the experiment (i.e., maybe they would have learned it had they been given more experience with the new values). Our results suggest otherwise, however, because the number of sessions in the second phase (Experiment 2) was not only more than the number of sessions in the original Gibbon and Church, but it was also greater than that of the initial experimental phase, suggesting ample opportunity for the task to be learned. A third, and more likely possibility, is that of retroactive interference. That is, it may be the case that experience with the initial FI values interfered with learning of the second set of FI values. If this is the case, then this suggests a limit on the cognitive capacities of mice not previously explored. Future research should investigate if this was truly the case, and whether there is a limitation on the number of values with which a particular mouse can be trained.

In conclusion, results of our experiments suggest that mice, in addition to rats and pigeons, can learn to respond according to the difference of temporal values, providing the first evidence of temporal subtraction in the mouse. Both experiments serve as a foundation for future investigations of the molecular foundations of non-verbal computations involving abstract values. In addition, our findings point to a possible limit on mouse cognition, suggesting that previous training values may interfere with future training, in contrast to earlier results with pigeons (Gibbon and Church, 1981). This pattern was not consistent across mice, however, indicating individual differences may play a part in this limitation.

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