A Probabilistic Model of Time Perception

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1 Introduction

The ability to perceive the passage of time is a crucial feature of the brain. Without this ability, it would be impossible to form meaningful relationships among changing spatial stimuli in order to gain useful knowledge about the world. Despite this fact, the question of how time is perceived and used in the brain has not been nearly as well-studied as perception and usage of spatial stimuli. This is perhaps because it seems easier to conduct very direct experiments with spatial stimuli, whereas experiments with temporal stimuli may be more difficult to design. The visual pathway has been explored extensively to discover the structure of receptive fields in neurons that are tuned to the orientations of edges, through such classic experiments as that of Hubel and Wiesel in 1962, among others [1] [2]. However, little is known about the mechanisms for processing timing of changes in the visual field, or any other area for that matter [3].

Temporal processing is thought to be carried out by different mechanisms based on the scale of the information being processed. It seems reasonable, for example, that the mechanism for detecting differences in the arrival times of sounds to each ear would be different than that for determining the cycles of circadian rhythms. In our work here we address the mechanism of perception of time at the scale of hundreds of milliseconds. Important real world tasks requiring information at this scale include speech generation and recognition, motion detection, and motor coordination, among others [4]. Can we create a biologically plausible mechanism for timing of events at this scale?

Many models have been proposed to answer this question and suggest possible mechanisms for the timing of events at this time-scale. The earliest models [5] rely on some kind of pulse counting timer, but these have experienced problems with generalization to novel tasks and in trying to model certain experiments. More recent models have explored state dependent networks, which have many nice properties which explain the effects of distractors seen in psychophysical experiments [3]. Here we present a probabilistic model for a timing mechanism which tries to capture the noise and uncertainty of perception seen in experimental data on various timing tasks. Our model falls somewhere between the traditional clock model and the state dependent network model. We hypothesize that our model could be viewed as a particular implementation of a certain kind of state dependent network, but this idea will be explored more fully in future work.

For the current work, our main goals are to develop the model, make sure it is biologically plausible, and show that it provides a reasonable explanation for data from two experiments. The first
experiment is that of the interval discrimination task performed with monkeys, which has shown that neurons in the posterior parietal cortex (area LIP) may be responsible for representation of elapsed time and that uncertainty in timing of events increases with the length of duration of the events, confirming the often found Weber law [6]. The second experiment was the interval production task performed with human subjects, which found that intervals presented in context (drawn from a specific distribution) biased the subjects’ perception of the intervals in accordance with the effect of a Bayesian prior based on the sample interval distribution [7].

2 Background

There are several critical ideas behind this project. First of all, since many experiments have demonstrated the existence of temporal processing in various areas throughout the brain [4], features that would make our model stronger are simplicity and the ability to be implemented in a general neural network. Therefore, we have designed a model that draws heavily on the properties of Markov chains, which achieve these features easily. Markov chains are defined by sequences of random variables, which can be thought of as states in a state space, that have the Markov property. This property basically asserts that future random variables in the sequence are conditionally independent of past variables given the present variable. More precisely, for a Markov chain over the random variables $V_1, V_2, ..., V_n$:

$$P(V_{i+1} = v | V_1 = v_1, ..., V_i = v_i) = P(V_{i+1} = v | V_i = v_i)$$

This property makes the Markov chain an ideal candidate for a simple neural network implementation because each random variable or state can be thought of as a neuron for which the only inputs are from one previous neuron. In the next section we will show more clearly how this could possibly be implemented.

Another key feature that our model should have is that uncertainty about the actual time should increase with the duration of time of a stimulus. This effect has been demonstrated in several experiments [4,6] and other experiments have further supported this by showing that the effect of prior context on timing estimation becomes more pronounced at longer time durations [7]. Our model does indeed achieve this behavior, which will also be explained in the next section.
3 Methods

In our model, knowledge of the duration of a stimulus event is represented as a probability distribution over a discrete set of \( n \) states in a Markov chain, \( S = S_1, ..., S_n \), each of which represents a time lapse of \( \tau_i \) milliseconds from the start of the stimulus. The states are assumed to divide the space of possible durations evenly, so

\[
|\tau_i - \tau_j| = |i - j| \delta \quad \forall i, j \in [1, ..., n]
\]

where \( \delta \) is some constant amount of time between each consecutive time state. A careful distinction must be made here to clarify the differences among the various measures of time in this model.

First of all, there is the actual continuous time in the real world. This real time is discretized to capture the limitations of neural processing in what we will call "experiment time". There is another discretization of real world time captured in \( S \) which we will call "model time". This "model time" is represented probabilistically as the model’s belief of how likely it is that each state represents the true "experiment time". In general the belief is a vector

\[
b_t = \begin{bmatrix} b_1 & b_2 & \ldots & b_n \end{bmatrix}
\]

where \( t \) refers to the "experiment time" and each element \( b_i \) in the vector indicates the probability that the stimulus has lasted an amount of time in the interval \([\tau_i, \tau_{i+1}]\). When a stimulus is presented that is to be timed, the model starts with an initial belief distribution

\[
b_0 = \begin{bmatrix} 1 & 0 & \ldots & 0 \end{bmatrix}
\]

over the time states. As the stimulus continues, belief propagates from shorter to longer time states. This is accomplished via a network implementing the Markov Chain discussed earlier as shown in Figure 1(a) in which each state transitions to the next state with probability \( p \), or stays in the same state with probability \( 1 - p \). This transition model is represented in a matrix, \( T \), which has the probability for staying in the same state at each element along the main diagonal and the probability for transitioning to the next state along the diagonal directly above the main:

\[
T = \begin{bmatrix}
1 - p & p & 0 & 0 & 0 & \ldots & 0 \\
0 & 1 - p & p & 0 & 0 & \ldots & 0 \\
0 & 0 & 1 - p & p & 0 & \ldots & 0 \\
0 & 0 & 0 & \ddots & \ddots & \ddots & \ddots \\
\vdots & \vdots & \vdots & \ddots & \ddots & \ddots & 0 \\
\vdots & \vdots & \vdots & \ddots & \ddots & \ddots & 1 - p & p \\
0 & 0 & 0 & \ldots & \ldots & \ldots & 0 & 1
\end{bmatrix}
\]

The reason for the last element being 1 is so the belief vector always sums to 1, which will become clear soon. Because of this, the last element of the belief vector, \( b_n \), actually represents the probability that the stimulus has lasted for some time in the interval \([\tau_n, \infty)\). The propagation of belief, depicted graphically in Figure 1(b), happens through repeated multiplication of the belief vector by the transition matrix. So the network’s belief vector at experiment time \( t \) can be calculated as:

\[
b_t = b_0 T^t
\]

or as an update from the previous belief state:

\[
b_t = b_{t-1} T
\]
Figure 1: (a) This is an illustration of the graphical structure of our Markov chain timer. As time progresses, the model’s belief of the amount of time that has elapsed propagates from low states to high states. At each time step, each state in the model transfers some of its current belief to the next state while retaining the rest of its belief. Specifically, if the current belief at state $i$ is $b_i$ and the current belief at state $i+1$ is $b_{i+1}$, then after one time step, the belief at state $i$ is now $(1-p)b_i$ and the belief at state $i+1$ is $pb_i + (1-p)b_{i+1} - pb_{i+1}$. (b) This graph shows three example belief states from the model as it times an event from 0 to 1600 ms. In this case the time step for transitions in the model was set to 1 ms. The belief state is depicted at 100 ms with the blue curve, at 800 ms with the green curve, and at 1600 ms with the red curve. There are two main features to notice from this figure. First of all, the maximum of each belief state occurs at the correct time of either 100, 800, or 1600 ms. Second of all, it is clear that uncertainty increases as time progresses because the width of the curves increases. These properties suggest that our model at least works to tell time and also captures the uncertainty seen in empirical data.
3.1 Biological Plausibility

In terms of biological plausibility, this model basically encodes a simple neural network defined in terms of firing rate dynamics. An illustration of a possible network implementation is shown in Figure 2. In this case the dynamics of the neural network would be governed by the general equation for recurrent neural networks, with the connection matrices set to encode the edges in the figure:

\[ \tau \frac{dv}{dt} = -v + F(Wu + Mv) \]

The time constant \( \tau \) is governed by the time step setting in the Markov chain.

Figure 2: (a) Neural network for a Markov chain.
4 Results

We tested our model’s performance in reproducing results from several important experiments in the time perception literature. The first is the interval discrimination task and the second is the interval reproduction task. Here we will explain these experiments and how our model offers an explanation for the behavior of subjects observed in the experiments.

4.1 Interval Discrimination Task

In this experiment [6] monkeys were trained to perform the task shown in Figure 3(a). In our model, this experiment can be simulated in a very straightforward way. Our goal is to obtain the probability of the monkey reporting “longer” for many different test cues. First, we simulate the timing of the standard cue by starting with an initial belief vector and multiplying repeatedly by the transition matrix, \( T \), for the number of discrete timesteps, \( c \), equivalent to the length of the standard cue. This produces a belief representing the subject’s uncertainty as to how long the cue actually lasted, but it will have a mean around the time state representing the standard cue:

\[
b_c = \begin{bmatrix} b_1 & b_2 & \ldots & b_n \end{bmatrix}
\]

Next we simulate the timing of the test cue in a similar manner with repeated multiplication of the belief vector by \( T \) for \( t \) timesteps corresponding to the length of the test cue, producing a final belief vector for this interval:

\[
b'_t = \begin{bmatrix} b'_1 & b'_2 & \ldots & b'_n \end{bmatrix}
\]

From these two belief vectors, we can obtain the probability of reporting “longer” as:

\[
P(d = d_L) = \sum_{i \in [1,n]} P(d = d_L | c = i) P(c = i)
\]

\[
= \sum_{i \in [1,n]} P(c = i) \sum_{j \in [i,n]} b'_j
\]

\[
= \sum_{i \in [1,n]} b_i \sum_{j \in [i,n]} b'_j
\]

The inner sum is just the total belief of the length of the test cue for time states longer than each possible standard cue, \( i \). The probability that the standard cue was represented by state \( i \) is simply just the belief over the standard cue at state \( i \).

To evaluate our model, we compared our probability of reporting longer to the empirical probability of reporting longer obtained by Leon et al. Figure 3(b) shows our model result and the experimental result for both standard cues tested in the experiment.
Figure 3: (a) Graphic from [6]. Interval discrimination task: In each trial the subject starts by fixating on a blue dot in the center of the screen. Then the dot changes to white for some amount of time $c$, which is called the "standard cue". Then the dot goes back to blue for some delay time before turning white again for a certain time, which is called the "test cue". Finally, the dot turns blue for some delay time and then goes away, at which point the monkey has to decide whether the test cue had a shorter or longer duration as compared to the standard cue duration. The monkey indicates its decision $d \in \{d_S, d_L\}$ with a saccade to either the green circle in the lower right $d_S$ (meaning "shorter") or the red circle in the upper left $d_L$ (meaning "longer"). (b) Probability of monkey reporting longer for our model (blue) and from the data (green) for two different standard cues (316 and 800 ms) and for many different possible test cues (ranging from 0 to 1600 ms). The mean squared error (MSE) between our model and the data from [6] for the short standard is 0.00014 and the MSE for the long standard is 0.00052. (c) Standard deviation vs. mean of belief distribution for time intervals ranging from 100 to 1600 ms. This result agrees with the commonly observed Weber Law that standard deviation scales approximately proportionally with the mean.
4.2 Interval Reproduction Task

In this experiment [7] humans performed the task illustrated in Figure 4(a). The main result of this experiment was that the brain relies on prior context in order to aid in the perception of time intervals. Therefore, if the intervals during a specific set of trials are drawn from a set distribution, the reproduced intervals will be skewed towards the mean of the sample interval distribution, as shown in Figure 4(b). To simulate this experiment in our model, we first obtain a belief over the sample interval through the methods described above:

\[ \mathbf{b}_c = \begin{bmatrix} b_1 & b_2 & \ldots & b_n \end{bmatrix} \]

Then, we obtain a belief over the mean interval of the distribution of the sample intervals:

\[ \bar{\mathbf{b}}_t = \begin{bmatrix} \bar{b}_1 & \bar{b}_2 & \ldots & \bar{b}_n \end{bmatrix} \]

The effect of the prior belief over the sample intervals is obtained by element-wise multiplication the two belief vectors above, followed by a maximum a posteriori (MAP) estimate to produce the most probable interval:

\[ b_{\text{posterior}} = \mathbf{b}_c \odot \bar{\mathbf{b}}_t \]

\[ \hat{c} = \arg \max_i (b_{\text{posterior}}[i]) \]

This gives a new estimate for the production time which is skewed in favor of producing intervals closer to the mean of the sample interval distribution. To evaluate our model, we tested several interval distributions. The Figure 4(c) shows the resulting bias effects from the prior. This particular method of applying the bias is the MAP estimate for the production time. However, in [7] it was found that the Bayesian least squares estimate was much closer to actual human performance on the task. This may be the reason that our current model does not seem to account for increased uncertainty and increased influence of the prior at longer time intervals (notice that each production time line in Figure 4(c) is sloped approximately by the same amount, whereas the results from human experiments showed decreased slope at longer times).
Figure 4: (a) Graphic from [7]. In each trial subjects started by fixating their gaze on a central dot and after one second a feedback dot would appear to the left. Then after a random delay, a "ready cue" appeared followed later by a "set cue". The subjects were instructed to reproduce the interval between the ready cue and set cue immediately after the set cue terminated. The produced interval was designated as the time from the set cue to when the subjects pressed a button indicating the end of the production interval. (b) Graphic from [7]. The original result showing that when intervals are presented in the context of distributions with different means, the resulting production interval will skew towards the mean of the sample distribution. There are 3 distributions used in this experiment (short, intermediate, and long) which are depicted in the corner of the figure to the left. (c) Our results showing a similar effect if a prior belief is in effect during the interval reproduction task.
4.3 LIP responses during Time Discrimination

Neurons in various areas of brain have been shown to encode the probability that a decision will ensue \[8\]-\[10\]. Especially neurons in the lateral intraparietal area (LIP) have been thought to represent the expected outcome of decisions that result in eye movement responses. Since in the perceptual decision making tasks of monkeys, the expected gain of an eye movement is just the reward multiplied by the probability of the corresponding decision being selected, we hypothesized that the persistent activity of LIP might encode the probability that an action will be chosen in the next time step. In the context of time interval discrimination tasks, we hypothesized that LIP responses encode the probability that the test cue duration is longer than the standard one if the next time step were the end of the test cue: \(LIP^L(t) = P(d = d_L)\). The LIP response for neurons representing shorter targets is defined similarly.

In figure 5, we compare the experimental (left) LIP activities with model predictions (right). Solid and dashed curves represents trials with 800 ms and 316 ms standard cues, respectively. Red and green curves exhibit the LIP responses with long \(d_L\) and short \(d_S\) targets in the corresponding receptive fields, respectively. Our simulation data didn’t aim to provide a quantitative fit to the experimental data. However, our model prediction captures several important qualitative features of the neural data. First, neurons reporting \(d_L\) longer targets show increasing firing rates while neurons reporting \(d_S\) shorter targets show decreasing responses, consistent with the experimental data. Second, a decision is made when the responses reach a fixed boundary, similar to bounded activities in LIP. Last but not least, the crisscrossed pattern of neural activity was evident in our model simulation.

Figure 5: LIP Responses during an time interval discrimination task. (a) shows the average normalized response from 54 LIP neurons reported in \[6\]. Solid and dashed curves represents terminate trials with 800 ms and 316 ms standard cues, respectively. The red and green curves represent LIP responses favoring long \(d_L\) and short \(d_S\) targets in the corresponding receptive fields, respectively. (b) The model LIP responses compute the probability that the cue duration is shorter (green) or longer (red) than the standard cue if it were to terminate in the next time step. Solid and dashed curves represents trials with 800 ms and 316 ms standard cues, respectively. The cross-over pattern observed in our model simulation is characteristic of the experimental neural responses in area LIP.
5 Conclusions

Our results suggest that time perception in the brain at the millisecond scale may be accomplished via a probabilistic timing mechanism that would be easily implemented in a network of neurons. The mechanism uses a simple Markov chain model in which the value of each state encodes the model’s belief that the actual elapsed time is within the time window represented by the state. The model provides a unified explanation for experimental data from two different tasks, although for the second task, some adjustments must be made to achieve the exact results seen in the human data. However, the model predicts the amount of uncertainty in the interval discrimination task well and shows the general behavior desired for the effect of a prior distribution over sample intervals in the interval production task.

This model has great potential to be expanded in future work. In particular, a more detailed version could be created using integrate and fire neurons to more accurately match the data from LIP neurons. Also, the connections of our model to the state dependent networks discussed in other works [3] could be explored to unify the models. In addition, there are more time perception experiments to be explained. For example, studies have shown that humans can improve and learn on the interval discrimination task [11][13]. In our model this could possibly be represented by an initial amount of noise in the transition matrix dynamics which, over time, decreases to enable the model to achieve better performance. Therefore, we envision that the current model could be encapsulated in a partially observable Markov decision process (POMDP) to enable fine tuning of the transition matrix dynamics though temporal difference (TD) learning, a mechanism designed to model the dopamine system in the brain, which has been explored in previous work [14][15].

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References


