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Neurocomputational models of interval and pattern timing

Nicholas F Hardy and Dean V Buonomano

Most of the computations and tasks performed by the brain require the ability to tell time, and process and generate temporal patterns. Thus, there is a diverse set of neural mechanisms in place to allow the brain to tell time across a wide range of scales: from interaural delays on the order of microseconds to circadian rhythms and beyond. Temporal processing is most sophisticated on the scale of tens of milliseconds to a few seconds, because it is within this range that the brain must recognize and produce complex temporal patterns — such as those that characterize speech and music. Most models of timing, however, have focused primarily on simple intervals and durations, thus it is not clear whether they will generalize to complex pattern-based temporal tasks. Here, we review neurobiologically based models of timing in the subsecond range, focusing on whether they generalize to tasks that require placing consecutive intervals in the context of an overall pattern, that is, *pattern timing*.

Address
Departments of Neurobiology and Psychology, and Integrative Center for Learning and Memory, University of California, Los Angeles, Los Angeles, CA 90095, United States

Corresponding author: Buonomano, Dean V (dbuono@ucla.edu)

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Introduction

The dynamic nature of our environment and the need to move, communicate, and anticipate *when* events will happen, contributed to the evolution of neural mechanisms that allow the brain to tell time. On one extreme, animals detect the microsecond delays it takes sound waves to travel from one side of the head to the other in order to localize sound sources in space [1]. On the other extreme, circadian rhythms allow animals to track day–night cycles in the absence of external cues [2,3]. Between these extremes, humans and other animals also time events on the order seconds to minutes. Humans, for example, anticipate the duration of traffic lights or the time between telephone rings. Similarly some animals track the amount of time between visits to food sources in order to optimize foraging [4,5]. Finally, rodents and other animals can be trained on a diverse range of temporal tasks, such as peak interval procedures in which they learn the interval between a stimulus and reward availability [6–8].

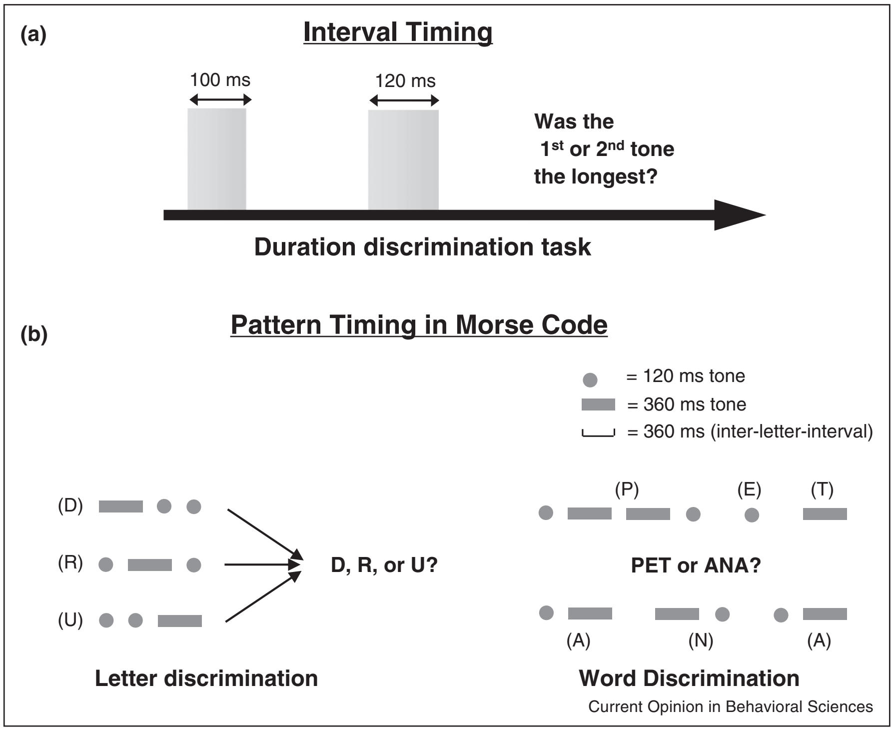
In the above examples, animals primarily need to time isolated intervals or durations, as opposed to complex temporal patterns defined by the relative timing of multiple consecutive intervals. The prosody of speech and the rhythm of music, for example, are not defined by any single interval or duration, but by the global temporal structure of many consecutive intervals. Furthermore, speech and music require timing multiple embedded temporal patterns. For example, voice-onset time (the interval between air release and vocal cord vibration) contributes to phoneme discrimination [9], the duration of vowels and pauses between words conveys information about phrase boundaries [10,11], and speech rate and contour contribute to prosody and comprehension [12–14]. Thus speech relies on timing over a number of different scales and features in parallel.

Perhaps the clearest example of just how sophisticated our ability to process complex temporal patterns can be is that language is reducible to a purely temporal code. Specifically, when individuals communicate via Morse code, the information is contained in the duration of tones, the interval between them, and their global structure. At the relatively low speed of 10 words-per-minute each dot and dash is 120 and 360 ms long respectively, and the inter-letter and inter-word intervals are 360 and 840 ms. The offset of any tone marks the stop time of a duration and the start time of an interval. This fact helps constrain the possible timing mechanisms underlying Morse code recognition, as any mechanism that requires a significant amount of time to 'reset' before timing the next interval, would be unlikely to satisfy the temporal requirements of Morse code.

To distinguish between temporal tasks that require timing isolated intervals from those that require timing multiple consecutive intervals within a global context, we will use the terms *interval timing* (although we note that this term is commonly used for timing in the range of seconds to minutes [6]) and *pattern timing* (Figure 1).

While most psychophysical tasks focus on interval timing, a number of temporal tasks rely on the production or

Figure 1



Interval versus pattern timing. **(a)** In a duration discrimination task subjects listen to two tones of different durations, and are asked to determine which is longer. Interval discrimination tasks are very similar, except that the temporal extent of each stimulus is demarcated by the interval between two brief tones. **(b)** Communicating with Morse code requires pattern timing. Discrimination of the letters D, R, and U, requires paying attention to the timing of each tone (is it a dot or a dash?), as well as the position of the dash within the overall pattern **(Left)**. Discrimination of the words PET and ANA also relies on determining the duration of each tone, but here the overall sequence of dots and dashes is the same. The distinction between the words is coded in the position of the longer inter-letter intervals **(Right)**.

discrimination of intervals embedded within a global pattern. Such tasks include:

1) ***Temporal pattern reproduction:*** The motor production of a sequence of different intervals [15–17].
2) ***Serial reaction time task***: This task is a form of implicit timing in which subjects are required to press an array of keys that light up at specific times in a specific order. With practice the reaction times to press each key decrease [18,19].

To simplify our discussion, we will focus on aperiodic patterns as opposed to periodic tasks in which subjects have to discriminate or reproduce isolated or repetitive intervals [20]. However, there is data suggesting that periodic and aperiodic timing tasks rely on different neural mechanisms [21,22].

It is clear that the brain uses multiple neural mechanisms to tell time across temporal scales. For example the mechanisms underlying sound localization, the ability to tap along with the beat of a song, or generate circadian rhythms are clearly distinct [23,24]. However, it is less clear whether the neural mechanisms underlying interval and pattern timing are the same: does pattern timing rely on the timing of independent intervals, like marking the laps on a stopwatch, or is each interval automatically encoded in the context of a pattern? Here we ask if the same mechanisms that have been proposed to underlie simple forms of timing can also account for the complex temporal tasks such as recognizing and producing letters in Morse code. To answer this question we examine three classes of neurobiologically-based timing models — that is, those that have been implemented at the level of simulated neurons (spiking or firing rate).

Synfire chain models of timing

One of the simplest models of how time might be represented in networks of neurons is a *synfire chain*, which is generally composed of a large number of neurons arranged in separate pools connected with a feed-forward architecture (Figure 2) [25–27]. Activity propagates from one pool to another, such that each pool is activated at different points in time — for example, pool one is activated at $t = 0$, while neurons in pool 10 might be activated