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A single mechanism account of duration and rate processing via the pacemaker-accumulator and beat frequency models

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Abstract

Time is an essential dimension of our environment that allows us to extract meaningful information about speed of movement, speech, motor actions and fine motor control. Traditionally, models of time have tried to quantify how the brain might process the duration of an event. The most commonly cited are the pacemaker-accumulator model and the beat frequency model of interval timing, which explain how duration is perceived, represented and encoded. Here we posit such models as providing a powerful tool for simultaneously extracting, representing and encoding stimulus rate information. That is, any model that can process duration has all the information needed to code stimulus rate. We explore different processing strategies which would enable rate to be read off from both the pacemaker-accumulator and beat frequency model of interval timing. Finally we explore open questions that, when answered, will shed light upon potential mechanisms for duration and rate estimation.

Keywords

Temporal processing; duration; rate; pacemaker-accumulator model; beat frequency model; unified mechanism

Introduction

Our perception of the world around us is essentially informed by our ability to code time; speech and music provide just two examples of processes in which perceiving the temporal extent of an event, and dividing the event into substructures is essential to perception of the stimulus. To be able to make sense of such complex stimuli, the brain needs to be able to extract both duration and rate information. The process by which we are able to construct representations of temporal content remains poorly understood and the experimental

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literature is rife with contradiction. Here we propose why and how temporal extent (duration) and temporal frequency (rate) may be subserved by the same mechanism.

A complete model of time perception should be biologically plausible, compatible with behavioural experimental data, and applicable across multiple timescales. Internal models of time perception have primarily been based on duration estimates, and often continue to be discussed only in the context of data about duration [1]. Here we suggest that information from rate experiments should likewise inform these models. Our contention is that the most efficient coding strategy for processing both duration and rate would be via a single mechanism. We focus on two prevalent models: the Pacemaker Accumulator (PA) model (Figure 1B), and the Beat Frequency (BF) model (Figure 1C), and demonstrate that both the PA and BF models can process duration and rate via a single mechanism, illustrating different ways in which rate and duration judgements would thereby co-vary. We also consider open questions in the field of time perception that will clarify whether there is a unified temporal mechanism (see Box 4).

We could, theoretically, have independent mechanisms for processing duration and rate information. However, duration and rate information are tightly linked; a mechanism that can compute one has all the necessary information to compute the other. Thus it is likely that the same temporal integration and memory mechanisms underlie both duration and rate discrimination [2]–[5]. Experimental evidence about single versus separable mechanisms for rate and duration is mixed. For instance, extensive work has been done in the Johnston lab [6] which demonstrates that, after matching for temporal frequency, a duration compression occurs independent of temporal frequency of the stimulus. The authors therefore argue duration effects are dissociable from rate, pointing to separate mechanisms. However, there are potential unified models that could account for their pattern of results (see [7] for further discussion of this point).

Pacemaker Accumulator Models

The PA model [8]–[11], has two main components: a pacemaker, which emits regular pulses, and an accumulator that counts the pulses. A switch turns the accumulator on or off, and a memory stage stores the output of the accumulator. This mechanism could be used to measure the duration of a single event or the elapsed time between events. To compare two durations, the switch would turn the accumulator on and off to count the pulses in the first duration, store the reading in memory, and then collect a new reading for the second duration. A decision stage would compare the remembered duration and the new duration to output a response of shorter or longer. Treisman showed that such a model can accommodate Weber's Law [9] and later refined his model to include a non-linear temporal oscillator for generating pulses [12].

How the PA might deal with rate as well as duration

A PA mechanism could deal with rate differently, depending on whether rate is processed on the “front end” or the “back end” of the model (see Box 3 Figure 2 for schematics of these two general approaches). Moreover, whether one posits single or multiple pacemakers and

whether perception is relative to an internal reference has important consequences for how a change in pacemaker frequency might influence perceived rate and duration as measured in behavioural studies. For instance, in single pacemaker models, relative judgements (as opposed to absolute judgements) may be unaffected by an increase or decrease in the pacemaker. Multiple pacemaker models allow for the possibility that some pacemakers change while others are unaffected (or that particular pacemakers do not all change in the same way), in which case relative judgements that draw upon different pacemakers would be changed, and only some absolute judgements would be affected.

The simplest PA models assume that the rate of a neurobiological process mimics the stimulus rate [12], [13]. We note, though, that this is the most naïve view of the relationship between content and vehicle (see [14] and for opposing views about whether this naïve view is plausible for time perception see [15] and [16]).

Evidence for single duration/rate mechanism (PA model)

There is behavioural evidence for a single, non-linear PA timing mechanism. For instance, Matthews manipulated tempo changes and showed that dynamic changes (whether increasing or decreasing over the course of an interval) led to duration overestimates [17], [18]. He suggested that the changes in tempo alter the rate of the accumulator. If so, there may be a non-linear relationship between accumulation rate and stimulus rate.

Recently, Horr & Di Luca provided further behavioural evidence; they found that intervals filled with rhythmically-grouped stimuli lead to an increased perceived duration as compared to intervals filled with irregularly-spaced beats. When they compared rhythmically-grouped to regularly-spaced beats with no additional rhythm, there was no compression or expansion of elapsed time [19]. Consistent with a single mechanism for perceived duration and rate, the number of beats in the interval also modulated perceived duration, showing a compression in perceived duration for increasing number of stimuli. The PA model accounting for rate predicts perceived duration to decrease with increases in number of rhythmic beats in the interval.

Beat frequency models

The BF model of interval timing posits that durations are encoded by ensembles of neurons, oscillating at different frequencies, that are reset and synchronized at the onset of the “to be timed” stimulus [20]. Because there are many possible sub-ensembles of a collection of neurons, a wide range of durations can be encoded and differentiated (see Figure 1C). Striatal medium spiny neurons could plausibly carry out these computations [21], and evidence from lesion and neuroimaging studies is consistent with the notion that these brain areas are involved in timing [22]–[25]. There has been a great deal of recent interest in applying these models to behavioural data [11], [26]–[31].

How BF model might handle rate and duration

The BF model could handle rate in several ways, the most obvious corresponding to whether rate gets processed on the “front end”, via a correlation between rate of the stimulus and

frequencies of the oscillators: by altering frequencies and/or amplitudes of the oscillators or of sub-collections of oscillators. By reading out the frequencies of the oscillators suitably correlated to the stimulus, stimulus rate would be returned. Judgements of duration would be influenced by stimulus-driven oscillations if a sub-ensemble's beat frequency is thereby changed. If this were the means by which rate and duration were simultaneously coded, then we would expect that a given stimulus duration (as gauged by an external time-keeper) will be estimated as different durations at different times, before or after adaptation (Box 3, Figure 3). In light of either potential strategy for coding rate, attention must be given to the nature of the temporal integration mechanism that could predict a specific pattern of co-variation of rate and duration judgements, and adaption or entrainment could have a number of different possible effects.

The “front end” picture (see Box 3, Figure 3) gains plausibility from studies investigating the neural response to rhythmic inputs. Presentation of a rhythmic stimulus leads to entrainment of the neural oscillators to the beat frequency of the input. Stimulus rate for lower frequencies can therefore be read-off of changes in neural oscillation caused by entrainment. Both monkeys and human studies demonstrate this entrainment effect [32].

Teki et al. proposed a unified neural mechanism for perceptual timing (informed by both duration and rate) consistent with the predictions from the BF model. Perceived duration and rate are coded by coordinated activity in interconnected regions of striatal and olivocerebellar networks [31]. The site of their unified timer is primarily striatal. If the striatum performs both rate and duration processing then disruption of cerebellar mechanisms should leave rate and duration judgements intact; this is consistent with unimpaired rate and duration performance evident in cases of chronic cerebellar disruption [33]. This neurobiological evidence further supports the case for a single rather than dissociable mechanisms for rate and duration processing.

PA vs. BF: accounting for the influence of context

Many studies have observed context dependent distortions in perceived time [18], [34]. In the BF model, this can be explained by intervals correlated with oscillators that entrain to context rhythms, influencing judgements of subsequently presented stimuli [4], [34], [35]. As explicitly discussed by McAuley and Jones [34], a crucial characteristic of PA models is that the pacemaker phase ought to reset between a context stimulus and a comparison stimulus, while this is not an essential feature of the BF model. In the original incarnation of the BF model [20] oscillators were not reset prior to extraction of a duration estimate. Assuming the oscillators do not reset prior to a duration judgement, McAuley and Jones study provided behavioural evidence for a BF model processing strategy over PA models: they demonstrated negative effects of large changes in onset time of the comparison sequence on discrimination of different IOIs in the comparison sequence [34]. Further evidence, substantiating a change in neural response account of rate driven distortions in perceived duration, comes from Horr and Di Luca [36]. They manipulated the predictability of the rhythms in an interval and found that, consistent with BF predictions, changes in predictability alters the perceived duration via gain control mechanisms for predictable events.

Conclusions

More research will be required to test these modified duration/rate coding PA and BF models. A unified duration/rate coding PA model requires more modifications than its BF counterparts (see Box 3), and the inclusion of a non-linear temporal oscillator for generating pulses in the PA model makes the distinction between the two models less pronounced (see Box 3). Integrated models of time perception will make many commonplace predictions: for instance, that people can know that a light is flashing at a detectable rate and simultaneously estimate how long that flashing light was on for. But we suspect such models will also make surprising and apparently counterintuitive predictions. To determine whether our rate and duration timing mechanisms are integrated or not we will have to acquire much more data about the pattern of co-variation of rate and duration judgements and focus on more sophisticated models of temporal processing and multisensory integration [5], [30], [37]–[39]. But without opening up the space of possible timing models to include integrated mechanisms for rate and duration we risk casting our theoretical and experimental time perception net too narrowly in terms of identifying relevant biological and non-biological factors [40]. Consequently, we advocate a broader and more integrative approach in order to make progress on answering questions fundamental to knowing how it is that we perceive time.

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Box 1**Glossary****1. Unified versus Dissociable Mechanisms:**

A unified mechanism would perform all of the computations needed for different timing tasks, such as estimation of rate and duration. Dissociable mechanisms would calculate such properties separately, and may in part rely in different neural networks.

2. Rate:

The rate of a stimulus is defined as the periodicity of a stimulus over time, for instance, how quickly a light is flashing.

3. Duration:

Duration is the time that elapses between two markers, often the onset and offset markers of a stimulus. The duration judgement provides an estimate of how long a light is on.

4. Inter-Onset Intervals (IOIs):

The inter-onset interval is the difference in time between two successful “starts”. For instance, if a light is on for 13 ms, then off for 27 ms before turning on again, the IOI is 40 ms. The IOI is the inverse of the rate for a periodic stimulus.

5. Relative Judgements/Absolute Judgements:

A relative judgement is one made by comparing a stimulus to another stimulus or to a reference. For instance, intervals could be judged as long or short relative to some internal standard. An absolute judgement is made without reference to another stimulus, and might be used, for instance, in estimating time to contact.

6. Weber's Law:

The just noticeable difference (which is the amount that a stimulus has to be changed for the difference to be noticeable) between two stimuli is proportional to the magnitude of the stimulus. This has been particularly important in studies of duration perception.

7. Content/Vehicle:

Content: what is represented by an item. Vehicle: the item that does the representing. For a clock model to allow us to make judgments of duration (or rate) the clock model must have some (biological) state or states that represent a duration (or rate), leading us to make the judgement we do. The *content* of that representation is revealed by our judgment of duration (or rate), the biological state or states of the model that have this content are the *vehicle* of that representation. On a naive view of representing time, for example, the content (the judged duration or rate) is represented by a duration or rate of a biological process (the vehicle).

6. Beat Frequency:

The beat frequency refers to the oscillatory rate at which a subpopulation of in phase neurons respond, and the “beat period” defines the time span between consecutive moments at which the subpopulation of neurons respond in phase.

7. Striatal and olivocerebellar networks:

Both the striatal and the olivocerebellar networks have repeatedly been identified as contributing to the coding of duration and rate. The striatum is a portion of the basal ganglia that receives inputs from the entire neural cortex and has been proposed as a key part of the neural timing system, especially for the beat frequency model. Striatal medium spiny neurons fire in response to stimulation at different frequencies and are used for timing durations in the seconds to minutes time scales. The striatal network (striato-thalamo-cortical network which is composed of the putamen, caudate, thalamus, pre- SMA/SMA, premotor, and dorsolateral prefrontal cortex) responses are strongest when coding stimulus rate. The olivocerebellar network, comprising the inferior olive and the cerebellum, has been shown to be more active for duration-based timing.

8. Neural adaptation:

Neural adaptation refers to the change in some property of the response of a neuron or set of neurons over time, such as a change in firing rate due to repeated exposure to a particular stimulus.

9. Entrainment:

Entrainment occurs when neural oscillators synchronise their response to the frequency of an external stimulus. Entrainment is maximal at lower range beat frequencies.

Box 3**PA and BF model strategies for simultaneously coding rate****Coding of stimulus rate via the PA model**

1. A **“front end” strategy** for coding stimulus rate could be achieved by a correlation with the rate of the pacemaker itself. Rate judgments, relative or otherwise, would involve a “read out” of the pacemaker rate by the brain. This could be handled in the following ways:

- i. The PA model could incorporate a comparator unit that correlates stimulus rate with pacemaker rate to achieve a final rate judgement;
- ii. The PA model could involve several pacemakers and a cross-correlator component could compare across stimulus and pacemaker rates.

Adaptation: Repeated exposure to stimuli at a particular rate could change the frequency of the pacemaker (e.g., by changing the calibration unit) and thus adaptation to rate could speed up or slow down the pacemaker, and duration judgments and rate judgments would be adjusted accordingly.

In the case of (i) adapting to a higher rate would increase the pacemaker rate, leading to more pulses being emitted during a fixed stimulus duration, resulting in duration overestimation and underestimations of rate (relative to an unadapted state of the pacemaker); conversely, adaptation to a lower rate, would lead to underestimations of durations and overestimations of rate. In the case of (ii), it is plausible that only the pacemaker(s) of similar rate to the adaptor would be impacted by repeated exposure to a particular rate. The effect of adaptation would be limited to a narrow range, depending on the number of and tuning overlap between the pacemakers. Duration could be calculated by using a particular pacemaker working at a known frequency and counting the number of ticks that occur, and if that pacemaker is unaffected by the adaptation, this could lead to a situation where perceived duration is not influenced by a change in perceived rate.

2. A **“back end” method:** rate perception is simply a function of multiple duration percepts. The model initially computes durations from them, and sums to compute rate (see Gallistel & Gibbon, 2000). Given a series of flashes of light, each flash of light lasts a certain duration and the time between each flash, when the light is off, has a certain duration; the rate can be calculated by:
 - i. counting the number of flashes in a known interval of time,
 - ii. determining the period between successive onsets of the flashes and taking the inverse of this to determine rate, and/or
 - iii. measuring the durations of the flash and of the gap between flashes, combining them to determine the period of the sequence, and then taking the inverse to calculate rate.

Adaptation: In these cases, the simplest view would be to expect an inverse relationship between duration and rate; adaptation causing a perceived increase in rate would lead to a perceived decrease in duration. However, depending on whether the “known interval” is influenced by adaptation, it is possible that perceived rate could be unaffected by a change in perceived duration.

BF model

Incorporating rate estimates into the BF model of time perception

1. **The “front end” manner:** for oscillators that are suitably correlated with the rate of the stimulus, rate could be extracted via a read-out of active oscillator frequencies. If a sub-ensemble's beat frequency is altered by this then this would simultaneously influence duration estimates. For example, if a stimulus influences the frequencies of members of a sub-ensemble in quite different ways, such that the time between their successive in phase beats changes from 500 ms to 550 ms, then duration estimates driven by this sub-ensemble's striatal neuron will be quite different. That is, absent any other mechanism to correct for this kind of change, the striatal neuron that tracks this particular ensemble's beat frequency will be activated by different duration stimuli at some times than at others; sometimes that striatal neuron will be active for 500ms stimuli, at other times (after some kind of adaptation or entrainment) for 550 ms stimuli. Given this, we predict that the same physical stimulus duration (as measured by some external clock) will be judged to be of different duration on different occasions: 550 ms will be judged sometimes as 550ms, but after entrainment or adaptation, as 500ms.
2. **The “back end” processing of rate:** as a function of duration by detecting coincidences of striatal neurons themselves in response to a stimulus then computing the rate by a method akin to the “back end” processing for the PA model. Given either way of processing stimulus rate we can see that close attention to the nature of the temporal integration mechanism is required to predict a specific pattern of co-variation of rate and duration judgments, and one would have to devote considerable attention to the nature of the model before one could show that such a pattern disconfirmed it. As with the PA model, adaptation or entrainment may have different effects on different tasks; comparative judgements are likely to show different patterns of change than absolute judgements.

Adaptation: For the BF model, adaptation would result in a process akin to entrainment.

Box 4**Open Questions**

1. The brain is capable of timing intervals across a range of different time scales. How are the mechanisms underlying these time scales related to one another? Is the applicability of Weber's law across time scales due to an underlying set of common rules or computations or simply an emergent property of noisy neurons [28]? Are very long durations/slow rates timed in a different way from shorter durations/faster rates? Could it be that for a given time scale there is a common mechanism for duration and rate, but for another time scale the mechanisms are dissociable? Or are the mechanisms unified throughout the range of timescales humans perceive? And if the particular mechanisms for a given timescale (whether unified for rate and duration or not) are different mechanisms than those for another timescale, how do these mechanisms interact with one another. A systematic set of studies across a broad range of scales could help us assess the plausibility of the different models and their potential instantiations.
2. Judgements can be absolute or relative to an internal (or external) standard. Moreover, there could be several different internal standards operating at different time scales. Thus adaptation studies could play a particularly important role; by changing a standard and measuring perceptual consequences at different time scales, it may be possible to differentiate between possible timing models.
3. There are several recent studies looking at timing and multisensory interactions [41 – 49]. Timing could be modality-specific or could be independent of a particular sensory system. However, if rate and duration (and perhaps number) share a single underlying mechanism, then one might predict that whether that mechanism is multisensory should be the same across all tasks. Alternatively, some timing models may allow for certain components to be modality-specific while others are not (see [50] for discussion of some of these results). Moreover, any model will need to account for how information from different modalities is timed. Recent work directly comparing tasks, such as temporal order and simultaneity judgements, has shown that different patterns of data arise depending on what participants are asked to do [51], [52]. Multisensory studies of both rate and duration can, in tandem with a broad range of other tasks, help probe the plausibility of different models of temporal perception.

Highlights

- Duration data has dominated time perception theorising.
- Pacemaker-Accumulator (PA) and Beat Frequency (BF) models developed as duration models.
- Often overlooked, data on rate and covariation of rate and duration is important.
- We propose several ways to unify rate and duration processing in PA and BF models.

Figure 1.

Temporal events specified in terms of duration and rate and the models discussed as candidates for coding this information. A) Duration and rate for a periodic signal. B) The pacemaker-accumulator clock model. The different blocks represent different functional components of the model: pulses are produced at approximately equal intervals by a pacemaker. An accumulator that can be turned on or off, calculates the total number of pulses and integrate these over a specific time window. The output of the accumulator (a clock reading) for a given trial is stored in a memory component. The current trial clock reading is then compared to a reference memory stored template of previous readings via a final decision stage, to arrive at the duration judgement, e.g., longer or shorter. C) Beat-frequency model of event time. Ensembles of oscillating neurons code the incoming signal duration. These neurons reset and synchronize at the onset of the “to be timed” stimulus. At the criterion time ‘ d_t ’ (dotted vertical line), the phases of all oscillators are stored in reference memory, for later comparison. Given a collection of neurons oscillating at different frequencies, as time passes there will be instants at which sub-ensembles will be in phase (grey dotted line). The frequency at which a sub-ensemble is in phase is its “beat frequency”. These sub-ensembles code for the duration of an interval, the “beat period”, the interval marked by the time between consecutive instants at which they are in phase. The many sub-

ensembles of a collection can code numerous durations, and durations of lengths considerably longer than the frequency of any single oscillator in the ensemble.

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Figure 3. Methods by which the BF model could process rate in addition to duration