

# Encoding of Duration and Rate by an Integrative Model of Temporal Processing

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Several models of temporal processing have been proposed in the empirical literature on time perception; all have been developed as models of a single temporal property, primarily event duration. We argue that there is ample reason to expand upon these models in order to include the processing of both rate and duration. We describe several ways that two popular timing models could handle rate, and illustrate that they would lead to different patterns of co-variation of rate and duration judgments. We review evidence that seemingly indicates discrepancies between the manner in which rate and duration are processed, and show that this evidence is problematic. A failure to carefully consider more global models has led to overly hasty arguments derived from empirical results suggesting a necessary dissociation between mechanisms of rate and duration. We argue instead that these findings place important constraints on how a global model might function, but do not rule out a common mechanism for rate and duration judgment.

**Keywords:** Duration, rate, time perception, temporal integration, methodology of science

## I Introduction

While philosophy has had a long interest in time perception, the explanatory question that drives contemporary philosophers of cognitive science is how we construct a representation of the world that has the temporal content that it has (Callender, 2008; Dennett & Kinsbourne, 1992; Grush, 2007). Our representations of the world are rich with temporal content, but this is revealed by the empirical methods of the cognitive sciences, not armchair introspections of philosophers. Experiments reveal that we represent experiences as temporally ordered (e.g., Hirsh & Sherrick, 1961) or as simultaneous (e.g., Stone et al., 2001; see Vatakis et al., 2008 for discussion of the effect of task), and they tell us which kinds of stimuli and tasks will influence these temporal features of our representations. Similarly what has emerged is that we represent experiences as having temporal extent or rate: we are able to compare event

duration across a number of perceived events (e.g., Fraisse, 1984) or estimate rates of perceived stimuli (e.g., Fraisse, 1978), and well-described features of context have been shown to affect these judgments (e.g., Eisler, 1976; Matthews, 2011, 2013; McAuley & Kidd, 1998; McAuley & Jones, 2003). That our representations of the world are rich with temporal content is incontrovertible, but how we construct representations with the temporal content they have is far from well understood. A unified model of temporal processing should explain our judgments of temporal order, simultaneity, duration and rate at all time scales, but such a unified model of temporal processing is far off. Here we focus on experimental data about duration and rate, focusing on the ms-sec time scale. We define rate as the periodicity of a stimulus over time (including rhythmic processes), while duration is the elapsed time between two markers (such as onset/offset).

Several models of temporal processing have been proposed in the literature on timing and time perception;

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here we discuss just two: the Pacemaker Accumulator (PA) model, and the more recent Beat Frequency (BF) model. Both assume an explicit representation of time, although we do acknowledge that there is a body of research suggesting that these same temporal properties of the environment may be coded implicitly (see Ivry, 1996; Ivry & Schlerf, 2008; Karmarkar & Buonomano, 2007). We start with a discussion of constraints, both empirical and methodological, that we take to be natural constraints on any model of temporal processing. We then discuss different ways the PA and BF models could be used to process rate and duration, which leads to predictions about how rate and duration judgments co-vary. We then review empirical results on duration and rate perception that appear to show that the mechanisms for processing these different stimulus dimensions are dissociable, but, we argue that these results fail to establish this as a necessity for a variety of reasons. Our fundamental concern is that showing the ways in which duration judgments co-vary with rate judgments fails by itself to establish a dissociation of the mechanisms underlying these judgments without further argument that there is no (plausible) integrative model that can accommodate the pattern of co-variation of these judgments. We think the arguments for dissociation of rate and duration mechanisms have proceeded too quickly, without careful thought about how the body of evidence could be accounted for by a common mechanism.

## 2 Constraints on Clock Models

Models of time perception must have sufficient neurobiological plausibility (as evidenced by accommodation of lesion, pharmacological and neuroimaging data as well as discussion of feasibility of neurobiological implementation). They must be able to accommodate the evidence from psychophysical and psychological experiments. While all researchers in the field would agree that a complete theory of time perception should be able to accommodate all the data from time perception studies, we differ from much of the extant literature in our belief that data from different sorts of timing tasks should inform our building of models. Models of internal clocks that explain the mechanisms of time perception have been developed in response almost exclusively to data from duration experiments, and we think that this is a mistake. Information from rate experiments should inform the construction and assessment of these models if only because rate can be calculated by the number of events that occur per unit of time or the duration between stimulus onsets. We believe that an integrative model should account for the influence

of different types of timing tasks, and be able to accommodate and explain a richer array of temporal structure than just duration. It is our view that an efficient coding of temporal information should not require a plethora of separate mechanisms to cope with the temporal structure of the environment.

In principle we could have separate and independent mechanisms for processing rate and duration, but in the absence of a compelling case to suggest this, we think there are reasons to expect significant overlap and interaction between mechanisms underlying duration and rate perception. Our reason for this appeals to a form of Occam's razor. First, rate information provides duration information, so a mechanism that computes rate has at its disposal information to compute duration. But similarly, duration contains rate information, thus a mechanism that can compute duration can in principle compute rate. Any mechanism that relies on a rate processor, in a way that does not communicate with a duration processor or vice versa is unnecessarily costly for a neurobiological system. Rate and duration are intimately related; separate mechanisms for their processing are possible, but not as plausible as a temporal processing mechanism that can account for both.

Although largely overlooked, Meck et al. (1984) proposed that duration and rate discrimination involve the same temporal integration and memory mechanisms. This idea was based on the observations that duration and rate discrimination exhibit similar Weber fractions, are both bisected near the geometric mean of their anchor values, and are affected in a similar manner by hippocampal lesions. Church and Broadbent (1990) were more explicit in this suggestion and in an attempt to account for different temporal estimates such as elapsed time, number, and rate perception, they developed alternative models based, in part, on the mode-control model of timing and counting developed by Meck and colleagues (e.g., Aagten-Murphy et al., 2014; Hinton & Meck, 1997; Meck & Church, 1983; Meck et al., 1985). At its core, this model utilizes a pacemaker-accumulator mechanism stage for temporal integration as well as an alternative connectionist version of scalar timing theory (Gibbon et al., 1984, Church, 2003) involving multiple oscillators and an auto-association network. In addition, the theoretical framework of McAuley & Kidd (1998) and McAuley & Jones (2003) is compatible with our view: they probe judgments of duration in the context of rates of rhythmic patterns, but their model is only explicitly discussed as a model of duration perception. A key point of agreement between us, Church and Broadbent (1990) and McAuley & Kidd (1998) is that we believe, as they do,

that tempo discrimination and duration discrimination are fundamentally the same.

Implicit in the two leading models of duration processing we discuss below is an intimate relationship between duration and rate: both process duration via the processing of rate of some biological phenomenon, either via an explicit pacemaker or via neurons that oscillate or fire at a particular rate, and in both, rate and duration information rate are easily accessible (see Cordes, 2006; Cordes et al., 2007). For each we can see a number of ways to handle rate, which would give rise to different experimental predictions. As a consequence, we believe that rate and duration studies could show us that rate and duration are processed by separate and independent mechanisms. On the other hand, as we describe below, the majority of studies that have been conducted to date fail to convincingly establish separate mechanisms for the processing of duration and rate and may readily be accounted for by an integrative model of temporal processing and decision-making.

### 3 Two Clock Models

#### 3.1 Pacemaker Accumulator Models

The PA model of temporal processing has been a dominant model in the timing literature since the 1960's (Gibbon et al., 1984; Treisman, 1963, 2013; Van Rijn et al., 2014). While the details of the model have been filled out in a variety of ways, the rough outline of the model is as follows: During the clock stage, a pacemaker emits pulses at roughly regular intervals, and an accumulator or counter can be switched on and off in order to integrate the number of pulses over time. A memory stage stores the "clock reading" taken from the accumulator which represents the number of pulses integrated over time on a particular trial. A decision stage then compares the "clock reading" for the current trial with past clock readings for stimuli stored in reference memory, and a response is made, e.g., shorter or longer. Measuring the duration of a stimulus or the duration between two stimuli is achieved by the switch turning on and off at the appropriate time markers. Treisman's 1963 paper describes the basic model; pitched as an advantage is that it can accommodate Weber's law for duration: that the just noticeable difference between two durations is proportional to length of the base duration presented. To handle motor coordination in later instantiations of the model, the pacemaker itself is generated by a non-linear temporal oscillator whose pulses are adjusted by a calibration unit that can modify their frequency (Treisman et al., 1990).

This type of PA model is well known even if not universally endorsed. There are concerns about its neurobiological plausibility (Buhusi & Meck, 2005; Matell & Meck, 2000, 2004; Van Rijn et al., 2014): implementation of unbounded accumulation processes required to handle long enough durations is one concern, another is whether the model really delivers on its Weber's Law promises (e.g., Burr et al., 2009; Wearden, 2003). The changes in Weber fraction that occur when observers bisect very short temporal intervals (5-30ms) as compared to longer intervals (100-1000ms) are contrary to predictions from Weber's law: the Weber fraction for the shorter intervals is larger than that for longer intervals around 200ms (Burr et al., 2009, Wearden, 2003). While Burr et al. (2009) were not concerned with defining the rate of the accumulator, their results challenge Weber's law for duration estimation. As such, the model appears to fail to explain some basic properties of interval timing, at least for short intervals. We don't take these concerns to be insurmountable objections to the model; for example, one could have several timekeepers that work for different time scales and feed information to each other to handle unbounded accumulation, and by adding further modifications the model may be able to explain Weber's law for short intervals. And despite these worries, it enjoys a prominent place in the literature (Wearden, 2013). We are interested in how such a model could be used to process rate information, while remaining consistent with duration data.

There are a couple of plausible ways that a PA mechanism could handle rate corresponding roughly to whether rate is processed on the "front end" or the "back end" of the model. For the "front end" view, one could imagine rate of a stimulus to be represented by a correlation with the rate of the pacemaker itself. To get rate judgments, relative or otherwise, would require that we "read out" the pacemaker rate. This could be achieved in a number of ways. The PA model could have an additional comparator unit that compares the rate of stimulus with the rate of pacemaker to generate rate judgments. Or a PA model could function with several pacemakers, and rate judgments could track correlations between stimuli rates and pacemaker rates. In either case, 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 or slow the pacemaker, and duration judgments and rate judgments would be adjusted accordingly. In the case of a PA model with a single pacemaker, adapting to a higher rate would increase the rate of the pacemaker, which would lead to more pulses being emitted during a given fixed duration of a stimulus, resulting in

overestimations of durations 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 a multiple pacemaker model, it is plausible that only the pacemaker(s) of similar rate to the adaptor would be impacted by repeated exposure to a particular rate, so the effect of adaptation might be limited to a narrow range, depending on how many pacemakers are included in the model and whether they overlap in their tuning. 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. In our view this is the most naïve picture of how a pacemaker accumulator could handle rate perception. It assumes that rate of a stimulus is represented by rate of some neurobiological process in the brain (see Allman et al., 2014; Treisman et al., 1990; Wearden et al., 1999). This is certainly a possibility though it takes the most naïve view of the relation between content of a representation and the representing vehicle (for discussion of the importance of distinguishing content from vehicle see Dennett & Kinsbourne, 1992).

Another way that the PA model could handle rate would be on the “back end”: rate perception is simply a function of multiple duration percepts. The model initially computes durations and, from them, computes 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 (1) by counting the number of flashes in a known interval of time, (2) by determining the period between successive onsets of the flashes and taking the inverse of this to determine rate, and/or (3) by 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. 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.

In both the front end and back end views, the frequency of the pacemaker could change while perceptions of duration and perceptions of rate may or may not; if the percepts are calculated as relative properties (e.g., to some internal reference), then changes in the pacemaker frequency may actually cancel out. The issue of single

versus multiple pacemakers has potential consequences for what predictions are appropriate for a given task. If there is a single pacemaker, and participants are making comparative judgments, a change in pacemaker frequency may lead to no effect, while absolute judgments could be affected by the change. But in a multiple pacemaker model, comparative judgments could change if the stimuli being compared rely upon different pacemakers that do not all change in the same way, while absolute judgments might only change for the stimuli that stimulate the changed pacemaker.

Matthews (2011, 2013) investigated how changes in the tempo of a series of stimuli alters the duration that is read off by the perceiver. Three different temporal contexts were presented in which 1) the rate/duration of on- and off- durations in a total ‘to be estimated’ duration were equal, 2) the rate/duration decreased towards the end of the interval and 3) the rate/duration increased across the interval. Dynamically changing rates (conditions 2 & 3) lead to an over-estimation of total duration irrespective of the type of change. According to Matthews (2013), the changes in stimulus rate should alter the accumulation rate of the accumulator in a PA model. Given that the results demonstrate an overestimation of dynamically changing stimuli, irrespective of an increase or decrease in stimulus rate, this could suggest a non-linear relationship between accumulation rate and stimulus rate. In this instantiation of the PA, the accumulation rate could change with the stimulus, while the read-out duration would not be affected.

There is some debate as to whether our temporal processing is modality specific or multi-modal. We can imagine each modality having its own PA handling rate and duration in one of these ways, and a central interpreter that calculates duration and rate as a function of the inputs from the different modality specific clocks. Or we can imagine a mechanism that pulses at a rate that is determined by multi-modal integration, and accumulates these pulses centrally (see Allman et al., 2014; Buhusi & Meck, 2006, 2009; Chen & Zhou, 2014; Merchant et al., 2013).

### 3.2 Beat-Frequency Models

The BF model of interval timing has its origins in a seminal paper by Miall (1989). According to this model, durations are encoded by ensembles of oscillating neurons that are reset and synchronized at the onset of the “to be timed” stimulus. Given a collection of neurons oscillating at different frequencies, as time passes there will be instants at which sub-ensembles will be in phase. 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.

Miall intended this model as a proof of concept rather than the neurobiological underpinning of time perception: i.e., a neural network that works this way could code durations. Neurobiological plausibility comes via striatal medium spiny neurons which have been shown to function as the kind of coincidence detector required to track the beat periods of oscillating cortical and thalamic neurons (Matell & Meck, 2000, 2004; Matell et al., 2003), and lesion and neuroimaging studies seem to confirm the role of these brain regions in timing (e.g., Coull et al., 2011; Meck et al., 2008; Merchant et al., 2013). Neurobiological plausibility is a strength of the model, however a weakness of the model is its somewhat limited application to behavioural data from psychological and psychophysical experiments (Matell & Meck, 2004) – a concern that will undoubtedly be addressed over the course of time (see Aagten-Murphy et al., 2014; Allman & Meck, 2012; Buhusi & Oprisan, 2013; Lustig et al., 2005; Oprisan & Buhusi, 2011, 2013, 2014; Teki et al., 2012; Van Rijn et al., 2014).

The BF model also has close connections with some of the recent developments of dynamic attending theory (Jones & Boltz, 1989). In particular, context effects on duration judgments of inter-onset intervals (IOIs) in rhythmic sequences appear to be well explained by thinking of the timing of those intervals to be correlated with oscillators in something like a BF model (see in particular Jones & Boltz, 1989; McAuley & Kidd, 1998; McAuley & Jones, 2003). In this picture, oscillators in the context of rhythmic sequences can become phase shifted and entrained by context-generated rhythms, and this influences judgments of durations of IOIs in subsequently presented rhythmic sequences. An essential feature of the PA models that are discussed in particular by McAuley and Jones (2003) is that between a context stimulus and a comparison stimulus the phase of the pacemaker ought to reset, while no such resetting need occur in a BF model (this is not an essential feature of the BF model; as noted above, Miall’s original conception of the BF model does include a resetting of the oscillators prior to a duration timing). But, under this assumption their crucial experiment is one that shows negative effects of large changes in onset time of the comparison sequence on discrimination of different IOIs in the comparison sequence. These data provide some important psychological evidence that favours a version of the BF model over PA models.

Again, we can imagine several ways the BF model could handle rate, but the most obvious idea would be that rate gets processed on the “front end”, in terms of a correlation between the rate of the stimulus and the frequencies of the oscillators: either by altering their frequencies, or by altering the frequencies of sub-collections of oscillators. Here again, we are imagining that rate judgments are arrived at by a reading out of the frequencies of those oscillators that are suitably correlated with the stimulus. This will also influence duration judgments if a sub-ensemble’s beat frequency is thereby changed. 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, in the absence of 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. If this kind of thing happens we can also expect that the same 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. Or rate could be processed on the “back end” 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 judgments are likely to show different patterns of change than absolute judgments.

One perspective on neurobiologically plausible coding of rate, that lends its plausibility to the “front end” picture outlined above, comes from neuroimaging studies exploring responses to rhythmic input. What occurs within the stimulus presentation is entrainment of the neural oscillators to the beat frequency of the input. Rate can be estimated via the change in neural oscillation, that is, synchronisation to the stimulus. Neural substantiation of this coding of rate/rhythm has been demonstrated for monkeys and humans (e.g., Besle et al., 2011; Lakatos et al.,

2008; O'Connell et al., 2011). Entrainment is distinct from neural adaptation in that neural adaptation refers to the change in some property of response over time with a cost for the duration of the process that leads to fatigue of the neurons involved. However, entrainment is akin to the behavioural phenomenon of adaptation, which we discuss below in relation to rate and duration. To date there is no evidence to contradict the assumption that behavioural temporal adaptation may utilise such an entrainment at the neural level. An oscillator model of rate discrimination could read off the phase of the synchronised neural oscillations providing an estimate of rate for low-frequency oscillations.

## 4 Experimental Evidence

An integrative model of temporal processing will lead to predictions about the pattern of co-variation of rate and duration judgments; which pattern of predictions to expect depends on the nature of the model. There is a substantial amount of experimental evidence that has been taken to show that mechanisms for rate and duration processing are separate. We will review the following sources of evidence, by no means a complete coverage, that suggests rate and duration are separable: 1) adaptation data from vision, 2) studies of the subjective expansion of time, and 3) studies that, taken together, suggest that duration perception is sensory-specific, but that rate is not.

### 4.1 Visual Adaptation

Adaptation paradigms are one way to measure temporal perception. Johnston et al. (2006) presented participants with a sinusoidal grating that drifted back and forth. They found that when they used a grating that drifted relatively quickly (20 Hz), the perceived duration of a test grating (at 10 Hz) was reduced (whereas a 5-Hz adaptor had little effect). They found the same pattern of results when they used a flickering adaptation stimulus that changed in brightness. We note that this result is contrary to the “naive” version of the PA model, as that model would have predicted a lengthening in perceived duration, though it can be explained by more complicated PA models that allow for a negative aftereffect (e.g., a model with multiple pacemakers tuned to different frequencies could obtain a negative aftereffect if the adaptation causes pacemakers at frequencies similar to the adaptor to respond less vigorously). For both types of adaptation stimuli, they measured the effect on perceived temporal frequency and found that for both the 5-Hz and the 20-Hz adaptors, there was a significant negative aftereffect – that is, adaptation to the fast adaptor slowed down perceived temporal

frequency of a 10-Hz test stimulus, while adaptation to the slow adaptor increased the perceived temporal frequency of the test stimulus.

Johnston et al. (2006) argued that their pattern of results suggested that the duration effect could be dissociated from the frequency effect, for several reasons. First was perceptual consistency – they suggested that a reduction in perceived duration could be considered a form of temporal compression, and that such compression should also lead to an increase in perceived frequency; their results with the fast adaptor – a decrease in both perceived duration and perceived frequency – is incompatible with such an account. However, there are potential mechanisms for calculating rate and duration that would predict shifts in the same direction for duration and frequency. These data place an important constraint on potential models of temporal perception, but do not rule out a single rate/duration processor.

Second, Johnston et al. (2006) pointed out that their 5-Hz adaptor increased perceived temporal frequency, but did not change perceived duration. They take the result that perceived temporal frequency changes without any change in perceived duration to imply that temporal frequency and duration rely on separate neural mechanisms. However, when we examine the results of their adaptors together, we find that there is a plausible alternative explanation for this seeming dissociation. They actually collected data after exposure to three different moving grating adaptors: the 5-Hz and 20-Hz adaptors mentioned above as well as a 10-Hz adaptor (the same rate as their test stimuli). With the 10-Hz adaptor, they found a reduction in perceived duration and a “relatively minor” reduction in perceived temporal frequency and they do not provide an explanation for why this might occur. We note that the task in this study was a comparative one; participants saw gratings at two different locations, one on an adapted side, and one on an unadapted side of space, and judged the relative duration or relative temporal frequency of the two gratings. Participants saw adaptation stimuli on the adapted side, both during an adaptation phase and during “top-ups” between trials, and then (in random order) saw a 10-Hz, 600 ms standard stimulus on the adapted side and a comparison stimulus on the unadapted side; in duration experiments, this comparison stimulus was 10 Hz but of variable duration, and in the temporal frequency experiments, the comparison stimulus varied in temporal frequency. Thus the adapted side received far more total stimulation than the unadapted side. Duration perception for a location that has been repeatedly attended to could be different than for a location that has been less attended to, for reasons distinct from the particular temporal features of that stimulus. For

instance, either facilitation or inhibition of return can occur when two stimuli are presented sequentially in the same location; in this study the gap between adaptation and test trials was 500 ms, which an ISI at which inhibition generally occurs (Klein, 2000); Johnston and colleagues do not provide enough detail on their onset/offset experiment to determine whether inhibition of return might be occurring in their study. Because the 10-Hz adaptor (the same frequency as the test stimulus) did reduce apparent duration of subsequent stimuli at that location, simply looking at the change due to adaptation in the 5-Hz and 20-Hz conditions combines two effects: that from exposure to additional stimulation on one side (possibly an attentional effect) and that from exposure to the particular temporal properties of the adaptation stimuli. Comparing the effects of duration across all three adaptors, we see that adapting to 5 Hz leads to less reduction in perceived duration than adapting to 10 Hz, which in turn leads to less reduction than adapting to 20 Hz. Thus, relative to the “neutral” 10-Hz adaptor, the 5-Hz adaptor has influenced perceived location. Viewed in this light, the pattern of adaptation for duration and the pattern of adaptation for temporal frequency are actually similar in that, relative to 10-Hz adaptors, 5-Hz adaptors lead to reductions in perceived duration and perceived temporal frequency while 20-Hz adaptors lead to increases in perceived duration and perceived temporal frequency.

Third, Johnston et al. (2006) highlighted the results of their interval-reproduction experiment. In that version of the task, participants reproduced durations consisting of stimuli flickering at different rates. For 5-Hz stimuli, participants created durations that were shorter than the presented duration; for 20-Hz stimuli, they created durations that were longer than the presented duration, and they showed little bias in the 7-13 Hz range; thus the pattern was a tendency to see higher frequency stimuli as lasting longer. Johnston and colleagues argued this demonstrates that the reduction in perceived temporal frequency of the test stimulus would be unlikely to explain the duration after-effect, presumably because the effect of adaptation on perceived temporal rate was not large enough that it could explain the entire duration aftereffect. But here the authors used a very different paradigm and probed absolute perception of duration based on rate; there is no adaptation and the judgments are not comparative. In a later study, Matthews (2011) found that rating tasks and interval reproduction tasks lead to differences in perceived duration; it is plausible that a comparative judgment task would also yield different results from an interval reproduction task. Thus Johnston and colleagues’ experiments using these different tasks are not easily comparable; it could be that

adaptation to a particular stimulus causes a subsequent 10-Hz test stimulus in the adaptation location to be perceived as the same rate as, say, a 13-Hz stimulus, but this does not mean that the 10-Hz stimulus can be treated as equivalent to a 13-Hz stimulus. It is possible that multiple factors come into play with the adaptation paradigm: 1) an effect on perceived duration of adaptation to a particular frequency (the primary effect of interest in that paper), 2) an effect of location on perceived duration (which, as mentioned above, could be in part attentional), and 3) a tendency to perceive longer durations for stimuli of higher temporal frequency. The finding that the third factor is insufficient to fully explain the effect does not negate that it may play a role in the effect.

Finally, Johnston et al. (2006) added one more variation to their experiment to attempt to separate out temporal frequency and duration. Using the moving grating adaptors described above, they tested for perceived duration by exposing participants to a 5-Hz or 20-Hz adaptor, and then having them compare the 10-Hz, 600 ms standard to a comparison stimulus of variable duration that was 13 Hz (after adaptation to 5 Hz) or 7 Hz (after adaptation to 20 Hz). This manipulation was meant to equate the perceived temporal frequency of the standard and the comparison. They found the same basic effect as in their first experiments – the reduction of perceived duration for 20-Hz adaptors, but no substantial change for 5 Hz – and argue that rate is not the determining factor, as following 20-Hz adaptation, stimuli that are both oscillating at the same perceptual rate differ in perceived duration. Although we find this to be their most compelling argument, this result is not sufficient to fully dissociate the two effects. Participants could be using a different strategy here; by estimating reversals as a cue to duration, the 10-Hz stimulus would include more reversals and seem to be longer than a 7-Hz stimulus. Because the effects of having test stimuli at different frequencies was not systematically probed, and because we see that rate and duration could be processed by a single temporal integration mechanism in more than one way, there are many possible predictions. As a consequence, we believe that the primary conclusion of the paper – “duration adaptation is specific to a particular location” – stands. But we do not think the dissociation between perception of temporal rate and of duration has been established.

#### 4.2 Subjective Expansion of Time

The second area suggestive of dissociation between rate and duration perception comes from subjective expansion of time studies. Here an “oddball” stimulus that differs from a set of identical standards is perceived to last longer than the standards; even when the oddball is in the middle

of a sequence, and for a range of different stimulus dimensions, including colour, shape, and size. Moreover, this expansion can be found using a range of different psychophysical tasks (e.g., Tse et al., 2004). These results have been replicated by several other labs, and although there is no general consensus on the underlying explanation for the results, the findings are robust.

In contrast, whether an oddball stimulus has a different perceived rate than standard stimuli is less well established. Pariyadeth and Eagleman (2007) addressed this question by flickering photographs of everyday objects; oddball varied in the content of the picture. Standards were all flickered at 10 Hz, while the oddball could be one of a range of frequencies; participants showed no bias in determining the rate of the oddball. The authors conclude that subjective expansion of time does not influence perceived rate, but several lingering questions remain. There is no verification that the subjective expansion of time actually occurs with the flickering stimuli; they did not test these stimuli for changes in perceived duration. Flickering the photographs could essentially be repeating the picture multiple times, thus participants may have perceived the oddball stimulus as less odd. If rate is calculated using, for instance, the duration of time for which the stimulus is on, then after several cycles, participants might no longer be experiencing an oddball effect. In order to argue that rate and duration are properties that are processed by separate mechanisms, it is essential to use the same stimuli and measure both effects, and show that there is not a plausible temporal integration mechanism that can handle them both, so even if our concerns above were allayed by further experiments, an argument that the results could not be accommodated by a single mechanism that processed both rate and duration is needed.

### 4.3 Sensory Specificity

The last form of evidence that we will address comes from comparing data that suggest duration is a sensory-specific property (e.g., Heron et al., 2012) with data suggesting rate is not (e.g., Levitan et al., 2011). Heron and colleagues exposed participants to adaptor durations and found a negative aftereffect; exposures to repeated short intervals leads subsequent intervals to be perceived as longer (and the reverse for repeated exposure to long intervals), but this effect is tuned such that it is attenuated at large discrepancies between test and adaptor durations. They argue that their effect is sensory-specific; adaptation in one modality does not transfer to another. However, in their paradigm, headphones were used to present sounds, and so sounds were not co-located with their visual

stimuli. As duration adaptation seems to be location-specific (Johnston et al., 2006), it could be that the lack of transfer is not a result of a change in stimulus modality, but a change in spatial location. In the rate study, which co-located visual and auditory stimuli, there was crossmodal transfer of rate adaptation (Levitan et al., 2011). Further evidence for the importance of co-location of multisensory inputs on timing comes from Di Luca et al. (2009), who demonstrated a clear distinction in what is modulated, in their case by temporal recalibration, when stimuli are co-located or auditory stimuli are presented over headphones and visual stimuli from in front of the observer. In the latter case audition adapts and in the case of co-located audiovisual stimuli, vision adapts. Di Luca et al.'s data suggest that the implications for spatial co-location are non-trivial. So Heron and colleagues' claim of sensory specificity should be considered with caution. If their result were to hold with co-located stimuli, this would represent an important constraint on potential mechanisms for temporal perception, but without further discussion of potential mechanisms it still does not establish dissociation of the mechanisms for rate and duration. One older set of duration experiments (Walker et al., 1981) with co-located stimuli also suggests that adaptation does not transfer across the senses, but their adaptation paradigm induced a contingent aftereffect, where a pair of pulses of differing duration leads to a bias in reproducing the duration of a single pulse. It is not clear to us what mechanism leads to this phenomenon so we hesitate to speculate about whether the finding would also apply to more general duration aftereffects.

## 5 Conclusions

More research has to be done before we can draw firm conclusions about dissociation of mechanisms for rate and duration. An integrated model of time perception will surely have some predictions that we can describe with ease now: that when listening to the chiming of Big Ben at midnight, the first chime will be judged to occur before the second, and the time between the first and third chimes will be judged as shorter than the time between the third and the ninth, but such a model may have plenty of predictions we would take at face value to be counterintuitive. Models of temporal processing will have to accommodate evidence from psychophysical and psychological experiments, but to answer questions about integrated versus separate mechanisms for rate and duration requires consideration of more sophisticated models of temporal processing and multisensory integration (e.g., Allman et al., 2012, 2014; Cordes et al., 2007; Karmarkar, 2011; Matthews & Meck, 2014; Raposo et

al., 2012); these questions won't be decided by data alone. As we indicated above we think there are methodological reasons to think an integrated model of temporal perception is attractive, and we think future work would benefit from the development and testing of such models.

## 6 Authors' Note

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## 7 References

- Aagten-Murphy, D., Iversen, J. R., Williams, C. L., & Meck, W. H. (2014). Novel inversions in auditory sequences provide evidence for spontaneous subtraction of time and number. *Timing Time Percept.*, 2, 188-209.
- Allman, M. J., & Meck, W. H. (2012). Pathophysiological distortions in time perception and timed performance. *Brain*, 135, 656-677.
- Allman, M. J., Pelphrey, K. A., & Meck, W. H. (2012). Developmental neuroscience of time and number: Implications for autism and other neurodevelopmental disabilities. *Front. Integr. Neurosci.*, 6:7.
- Allman, M. J., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the internal clock: First- and second-order principles of subjective time. *Annu. Rev. Psychol.*, 65, 743-771.
- Besle, J., Schevon, C. A., Mehta, A. D., Lakatos, P., Goodman, R. R., McKhann, G. M., & Schroeder, C. E. (2011). Tuning of the human neocortex to the temporal dynamics of attended events. *J. Neurosci.*, 31, 3176-3185.
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nat. Rev. Neurosci.*, 6, 755-765.
- Buhusi, C. V., & Meck, W. H. (2006). Interval timing with gaps and distracters: Evaluation of the ambiguity, switch, and time-sharing hypotheses. *J. Exp. Psychol. Anim. Behav. Process.*, 32, 329-338.
- Buhusi, C. V., & Meck, W. H. (2009). Relative time sharing: New findings and an extension of the resource allocation model of temporal processing. *Philos. Trans. R. Soc. B.*, 364, 1875-1885.
- Buhusi, C. V., & Oprisan, S. A. (2013). Time-scale invariance as an emergent property in a perceptron with realistic, noisy neurons. *Behav. Process.*, 95, 60-70.
- Burr, D. C., Silva, O., Cicchini, G., Banks, M. S., & Morrone, M. C. (2009). Temporal mechanisms of multimodal binding. *Proc. R. Soc. B.*, 276, 1761-1769.
- Butler, J. S., Molholm, S., Fiebelkorn, I. C., Mercier, M. R., Schwartz, T. H., & Foxe, J. J. (2011). Common or redundant neural circuits for duration processing across audition and touch. *J. Neurosci.*, 31, 3400-3406.
- Callender, C. (2008). The common now. *Philos. Issues*, 18, 339-361.
- Chen, L., & Zhou, X. (2014). Fast transfer of crossmodal time interval training. *Exp. Brain Res.*, 232, 1855-1864.
- Church, R. M. (2003). A concise introduction to scalar timing theory. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 3-22). Boca Raton, FL: CRC Press.
- Church, R. M., & Broadbent, H. A. (1990). Alternative representations of time, number, and rate. *Cognition*, 37, 55-81.
- Cordes, S. (2006). Nonverbal rate computations in humans. *Diss. Abstr. Int. B*, 66(11-B), 6302.
- Cordes, S., Williams, C. L., & Meck, W. H. (2007). Common representations of abstract quantities. *Curr. Dir. Psychol. Sci.*, 16, 156-161.
- Coull, J. T., Cheng, R. K., & Meck, W. H. (2011). Neuroanatomical and neurochemical substrates of timing. *Neuropsychopharmacology*, 36, 3-25.
- Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. *Behav. Brain Sci.*, 15, 183-247.
- Di Luca, M., Machulla, T. K., & Ernst, M. O. (2009). Recalibration of multisensory simultaneity: Cross-modal transfer coincides with a change in perceptual latency. *J. Vision*, 9, 1-16.
- Eisler, H. (1976). Experiments on subjective duration 1868-1975: A collection of power function exponents. *Psychol. Bull.*, 83, 1154-1171.
- Fraisse, P. (1978). Time and rhythm perception. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception VIII: Perceptual coding* (pp. 203-254). New York, NY: Academic Press.
- Fraisse, P. (1984). Perception and estimation of time. *Annu. Rev. Psychol.*, 35, 1-37.
- Gallistel, C. R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychol. Rev.*, 107, 289-344.
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Ann. N.Y. Acad. Sci.*, 423, 52-77.
- Grush, R. (2007). Time and experience. *Philosophie der Zeit*, 27-44.
- Heron, J., Aaen-Stockdale, C., Hotchkiss, J., Roach, N. W., McGraw, P. V., & Whitaker, D. (2012). Duration channels mediate human time perception. *Proc. R. Soc. B.*, 279, 690-698.
- Hinton, S.C., & Meck, W.H. (1997). The "internal clocks" of circadian and interval timing. *Endeavour*, 21, 3-8.

- Hirsh, I. J., & Sherrick Jr., C. E. (1961). Perceived order in different sense modalities. *J. Exp. Psychol.*, *62*, 423-432.
- Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Curr. Opin. Neurobiol.*, *6*, 851-857.
- Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends Cogn. Sci.*, *12*, 273-280.
- Johnston, A., Arnold, D. H., & Nishida S. (2006). Spatially localized distortions of event time. *Curr. Biol.*, *16*, 472-479.
- Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, *96*(3), 459-491.
- Karmarkar, U. R. (2011). Defining the contributions of network clock models to millisecond timing. *Front. Integr. Neurosci.*, *5*:41.
- Karmarkar, U. R., & Buonomano, D. V. (2007). Timing in the absence of clocks: Encoding time in neural network states. *Neuron*, *53*, 427-438.
- Klein, R. M. (2000). Inhibition of return. *Trends Cogn. Sci.*, *4*, 138-147.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, *320*, 110-113.
- Levitani, C., Ban, Y. H. A., & Shimojo, S. (2011). What you see is what you just heard: The effect of temporal rate adaptation on human intersensory perception. *i-Perception*, *2*, 879-879.
- Lustig, C., Matell, M. S., & Meck, W. H. (2005). Not "just" a coincidence: Frontal-striatal synchronization in working memory and interval timing. *Memory*, *13*, 441-448.
- Matell, M. S., & Meck, W. H. (2000). Neuropsychological mechanisms of interval timing behaviour. *BioEssays*, *22*, 94-103.
- Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: Coincidence detection of oscillatory processes. *Cogn. Brain Res.*, *21*, 139-170.
- Matell, M. S., Meck, W. H., & Nicolelis, M. A. L. (2003). Interval timing and the encoding of signal duration by ensembles of cortical and striatal neurons. *Behav. Neurosci.*, *117*, 760-773.
- Matthews, W. J. (2011). How do changes in speed affect the perception of duration? *J. Exp. Psychol. Hum. Percept. Perform.*, *37*(5), 1617-1627.
- Matthews, W. J. (2013). How does sequence structure affect the judgment of time? Exploring a weighted sum of segments model. *Cogn. Psychol.*, *66*(3), 259-282.
- Matthews, W. J., & Meck, W. H. (2014). Time perception: The bad news and the good. *WIREs Cogn. Sci.*, doi: 10.1002/wcs.1298.
- McAuley, J. D., & Jones, M. R. (2003). Modeling effects of rhythmic context on perceived duration: a comparison of interval and entrainment approaches to short-interval timing. *J. Exp. Psychol. Hum. Percept. Perform.*, *29*(6), 1102-1124.
- McAuley, J. D., & Kidd, G. R. (1998). Effect of deviations from temporal expectations on tempo discrimination of isochronous tone sequences. *J. Exp. Psychol. Hum. Percept. Perform.*, *24*(6), 1786-1800.
- Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *J. Exp. Psychol. Anim. Behav. Process.*, *9*, 320-334.
- Meck, W. H., Church, R. M., & Gibbon, J. (1985). Temporal integration in duration and number discrimination. *J. Exp. Psychol. Anim. Behav. Process.*, *11*, 591-597.
- Meck, W. H., Church, R. M., & Olton, D. S. (1984). Hippocampus, time, and memory. *Behav. Neurosci.*, *98*, 3-22.
- Meck, W. H., Penney, T. B., & Pouthas, V. (2008). Cortico-striatal representation of time in animals and humans. *Curr. Opin. Neurobiol.*, *18*, 145-152.
- Merchant, H., Harrington, D. L., & Meck, W. H. (2013). Neural basis of the perception and estimation of time. *Annu. Rev. Neurosci.*, *36*, 313-336.
- Miall, C. (1989). The storage of time intervals using oscillating neurons. *Neural Comp.*, *1*, 359-371.
- O'Connell, M. N., Falchier, A., McGinnis, T., Schroeder, C. E., & Lakatos, P. (2011). Dual mechanism of neuronal ensemble inhibition in primary auditory cortex. *Neuron*, *69*, 805-817.
- Oprisan, S. A., & Buhusi, C. V. (2011). Modeling pharmacological clock and memory patterns of interval timing in a striatal beat-frequency model with realistic, noisy neurons. *Front. Integr. Neurosci.*, *5*:52.
- Oprisan, S. A., & Buhusi, C. V. (2013). How noise contributes to time-scale invariance of interval timing. *Phys. Rev. E*, *87*, 052717. <http://link.aps.org/doi/10.1103/PhysRevE.87.052717>
- Oprisan, S. A., & Buhusi, C. V. (2014). What is all the noise about in interval timing? *Philos. Trans. R. Soc. B.*, *369*, 20120459.
- Pariyadath, V., & Eagleman, D. (2007). The effect of predictability on subjective duration. *PLoS One* *2*(11): e1264.
- Raposo, D., Sheppard, J. P., Schrater, P. R., & Churchland, A. K. (2012). Multisensory decision-making in rats and humans. *J. Neurosci.*, *32*, 3726-3735.
- Stone, J. V., Hunkin, N. M., Porrill, J., Wood, R., Keeler, V., Beanland, M., ... Porter, N. R. (2001). When is now? Perception of simultaneity. *Proc. R. Soc. B.*, *268*, 31-38.
- Teki, S., Grube, M., & Griffiths, T. D. (2012). A unified model of time perception accounts for duration-based and beat-based timing mechanisms. *Front. Integr. Neurosci.*, *5*:90.

- Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock". *Psychol. Monogr.*, 77, 1-31.
- Treisman, M. (2013). The information-processing model of timing (Treisman, 1963): Its sources and further development. *Timing Time Percept.*, 1, 131-158.
- Treisman, M., Faulkner, A., Naish, P. L., & Brogan, D. (1990). The internal clock: Evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception*, 19, 705-743.
- Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Percept. Psychophys.*, 66, 1171-1189.
- van Rijn, H., Gu, B.-M., & Meck, W. H. (2014). Dedicated clock/timing-circuit theories of interval timing and timed behavior. *Adv. Exp. Med. Biol.*, 829, 75-99.
- Vatakis, A., Navarra, J., Soto-Faraco, S., & Spence, C. (2008). Audiovisual temporal adaptation of speech: Temporal order versus simultaneity judgments. *Exp. Brain Res.*, 185, 521-529.
- Walker, J. T., Irion, A. L., & Gordon, D. G. (1981). Simple and contingent aftereffects of perceived duration in vision and audition. *Percept. Psychophys.*, 29, 475-486.
- Wearden, J. H. (2003). Applying the scalar timing model to human time psychology: Progress and challenges. In H. Helfrich (Ed.), *Time and mind II: Information processing perspectives* (pp. 21-39). Kluwer, Dordrecht.
- Wearden, J. H. (2013). "From that paradise ...": The golden anniversary of timing. *Timing Time Percept.*, 1, 127-130.
- Wearden, J. H., Philpott, K., & Win, T. (1999). Speeding up and (...relatively...) slowing down an internal clock in humans. *Behav. Process.*, 46, 63-73.