# How Memory Mechanisms Influence Interval Timing: A Review

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Interval timing tasks can only be performed efficiently when the output of a clock system can be stored over a longer period of time, and be retrieved and reused during later trials. Although the importance of temporal reference memory for accurate timing has been acknowledged since the earliest theoretical work on interval timing, formal accounts of the role of memory in interval timing are fairly recent. An short overview is given of the first formal models in which memory effects were accounted for, followed by a review of the current theoretical approaches, which can be categorized on the basis of whether they assume a dynamic or static memory system.

From humans and other mammals to insects, animals have sought ways to benefit from temporal regularities in their environments, ranging from millisecond timing for proper motor control to circadian and infradian timing for adjustment to day-night or other long-term biological cycles. In between these two extremes is the timing of intervals that are relevant for cognitively controlled behavior, spanning durations from a couple of hundred milliseconds to minutes, often referred to as interval timing. Already the first modern theories of interval timing [see 1 for a recent review] proposed that a triad of cognitive processes underlie all behavior driven by interval timing. In these theories, a clock-system generates a value that systematically changes over time, a temporal reference memory system stores previously experienced durations, and a decision system determines how the current read-out of the clock-system relates to values stored in memory, and whether to take actions based on this comparison. The most prominent theories that adhere to this scheme are pacemaker-accumulator theories, which assume that temporal information, operationalized as the pulses emitted by a pacemaker, is accrued in an accumulator, analogous to the working of an hourglass. Interestingly, although alternative theories propose different mechanisms underlying the clock part, all theories assume and require a memory and decision system.

Perhaps unsurprisingly, most of the work on interval timing has focused on the clock part, and the memory and decision systems have typically played an auxiliary role. Recently, however, a number of new theories have been proposed that provide a detailed model the decision stage in an interval timing process [e.g., 2], that propose mechanisms that could explain how interval timing and memory processes interact [3], or that acknowledge that temporal cognition can only be accounted for by an interaction of general cognitive skills and the triad assumed by clock theories [4,5]. However, most literature simply assumes that a memory system holds a fairly stable and accurate representation of relevant durations that does not directly interfere with temporal performance, and takes a similar stance towards the decision component.

The lack of focus on the memory system is surprising as one of the best known empirical phenomena related to interval timing, Vierordt's law, is clearly driven by the way information is stored in memory [6,7]. Vierordt's law is most easily observed in experiments in which durations of different lengths are presented. When asked to reproduce such durations, the reproduced durations demonstrate a regression towards the mean with long durations underestimated, and short durations overestimated. Recent accounts of this phenomenon are typically based on the assumption that memory traces representing previously presented durations interfere with later temporal processing [6,8–10]. This regression towards the mean is observed even when the different durations easily distinguishable, for example when they are represented by unique, easily identifiable stimuli [11,12].

Vierordt's law demonstrates that although the importance of memory for timing has been acknowledged since the earliest work on interval timing, the formal theoretic accounts of the role of memory in interval timing are fairly recent. All these accounts assume that a perceived duration is affected by earlier perceived durations, but differ in their assumptions related to the processes underlying this biasing. In the remainder of this document, I will discuss three approaches that have been proposed to account for specific memory effects observed in interval timing tasks.

**Memory Mixing in Interval Timing**

The first systematic exploration of how the internal representation of earlier durations influences future estimation was reported by Penney et al [13]. Penney et al presented participants with a bisection experiment in which participants are presented a short and a long standard duration that they are asked to memorize, and then a series of comparison durations of which participants have to indicate whether they are more similar to the long or the short duration. The elegant manipulation in this experiment is that the comparison durations were either presented in the auditory or in the visual domain. As durations presented by means of an auditory signal are overestimated compared to durations presented as visual signals, one would expect that auditory presented trials have a higher proportion of “similar-to-long” responses than visually presented trials, which was indeed found when both modalities were presented in different blocks. However, if previous trials influence subsequent trials, a duration presented in the auditory domain should be perceived as shorter (and vice-versa for durations presented in the visual domain) in a condition in which trials of both modalities were presented in intermixed fashion. This pattern of results was indeed observed, suggesting that the memories of the auditory and visual durations are indeed mixed into one larger pool that influence subsequent responses, giving rise to the term “memory mixing”. Interestingly, the visual trials were affected by the auditory information to a stronger extend than vice versa.

Although this work pioneered the more detailed study of the role of the memory system on interval timing performance, no formal theory was provided on how specific traces of earlier temporal experiences influence subsequent performance. For example, this model does not account for trial-by-trial effects, as one might assume a differential response if a visually presented duration follows a sequence of stimuli presented in the same modality, than if it follows a sequence of auditory-presented durations.

Another question that was not addressed in this memory-mixing paper is how the veridical durations of earlier trials influence performance on subsequent trials – if memory plays such an important role, one would expect trial-by-trial effects with a previous short trial having a differential effect on the current trial than a previous long trial.

### Bayesian Memory Models of Interval Timing

A natural match to the notion that previous experiences influence later perceptual processes is the Bayesian approach in which the observed duration (called the likelihood) is weighted by the experience (the prior) to obtain a subjective percept (the posterior). The application of this approach has been popularized by a highly influential paper by Jazayeri and Shadlen [14] in which they present a Bayesian account of a phenomenon similar to the Vierordt effect. With their experiment, they demonstrated that when participants are asked to reproduce durations sampled from a small range of possible durations, a regression towards the mean can be observed that is larger for the longer durations than for the shorter durations.

The proposed Bayesian model accounts for this effect by assuming that already at the perceptual stage the input (i.e., the likelihood) differs as a function of the presented duration. That is, the explanation for the asymmetrical regression towards the mean hinges on the assumption that the purely bottom-up percept of a shorter duration is represented more accurately (i.e., a more narrow distribution) than that of a longer duration. The prior experiences exert their influence at the next stage, as the filter-like function of an uniformly distributed prior gives rise the observed asymmetry by truncating more of the long durations than of the short durations. Although the prior experiences play a critical role in this model, the model presented in the original work does not account for how the prior is learned or how it is amended over time. In other words, although the proposed model does take into account prior experience in an elegant, principled way, it needs to be extended to account for more dynamic memory effects, such as the influence of a trial immediately preceding the current trial. Moreover, the assumption of a uniformly distributed prior is an elegant simplification of the model, and well suited if the model focuses on explaining expert behavior (i.e., performance after extensive training), but is unlikely to account for data in more typical, less well-trained temporal tasks.

Acerbi, Wolpert and Vijayakumar [15] specifically focused on the prior, and assessed whether the prior would indeed reflect the properties of the environment. In their experiments, they presented either a higher proportion of short, or a higher proportion of long durations, or even sampled the presented durations from bimodal distributions. Although the priors that Acerbi et al reconstructed on the basis of the behavioral data did not perfectly mirror the empirical distributions, the results clearly indicated that the distribution of the prior roughly reflected the empirical distribution, and thus that the prior is indeed learned from prior experience. However, even this more elaborate model still assumes a static prior over the scope of the experiment, and thus does not incorporate any trial-by-trial effects. Although implementing a Kalman-filter, which could account for how the prior is updated on a trial-by-trial basis, is feasible [16], it has not been applied to the domain of interval timing as of yet [see for an alterantive approach, 17].

Nevertheless, the elegant and powerful mathematical properties of this type of model have allowed people to used the Bayesian approach as a tool to identify in what way subgroups in a population might differ based on individual differences, medical condition, or training [18,19].

### Trial-by-Trial Effects in Interval Timing

The simplest approach to account for trial-by-trial effects in interval timing is to assume that only the most recent trial influences the processing of the current duration. According to such an account, only a single trace needs to be stored in memory, which can be updated on every trial. Although some initial data seemed to support this notion [20], later work led the authors to conclude that such a perturbation account is probably to simplistic, and that older traces are likely to still exert some influence [21].

A more refined model for trial-by-trial effects applied to the domain of interval timing is the Internal Reference Model [IRM, 8,22] proposed by Dyjas, Bausenhart and Ulrich. According to this model, sharing some similarities with a Kalman filter [16], the perceived duration for the current trial ($I_n$) is a weighted average of the current duration ($D_n$) and an internal reference based on all previous durations ($I_{n-1}$): $I_n = g * I_{n-1} + (1-g) * D_n$, with *g* reflecting the relative weight of the current experience in relation to the previous experiences. As the perceived duration on trial *n* will be used as the internal reference on trial *n+1,* IRM's history of presented durations follows a geometrically moving average. This central feature of IRM allows this model to capture how the internal reference builds up during an experiment, and also allows for explaining how a memory representation can be build in experiments in which the presented durations generated from a non-stationary processes [22].

This model provides elegant and solid accounts for a number of phenomena related to memory effects in interval timing, including the Vierordt law [8]. At the same time, it only provides a functional description of how the memory system might work and, because of that, the IRM lacks the flexibility to account for more complex experimental setups, for example including multiple, separate streams of stimuli or feedback. An example of such a study is reported by Taatgen and Van Rijn [12] as in their experiment participants had to alternate between reproducing two durations of 2 and 3.2 seconds, with each stream represented by visually unique stimuli. The behavioral data was best fit by a model that assumed that a trial was mostly influenced by earlier encounters from the same stream, but that the alternative stream also exerted some influenced. This type of behavioral pattern is difficult to align with the IRM and Bayesian approaches that assume a static prior.

To account for their data, Taatgen and Van Rijn applied their earlier developed integrative timing model [4] to this task. According to this model, all previous encounters of durations are stored in a central memory store. Each encounter has an associated value reflecting its activation, a value that decreases of time. When a retrieval is initiated from memory, for example when a perceived interval needs to be reproduced, a blending process weighs the encoded durations by their activation values, and calculates an average. This way, older or less frequently presented durations will have a smaller influence that more recent, of very frequent durations. The basic version of this model is very similar to the IRM. However, by encoding, for example, the feedback that was provided when a certain duration was presented, or with what visual stimuli a duration is encoded, the blending process can weigh the encoded information for the similarity with the current context, and this can account for the role of the temporal reference memory story in more elaborate interval timing tasks. The notion that previous durations are encoded in memory traces that become less accessible over time is obviously a very generic approach, which allows for the application in many different contexts. For example, Los, Kruijne and Meeter [23] have recently proposed that hazard-rate effects in foreperiod studies can be explained by assuming a trace-based memory system of previously experienced foreperiods, recent theories that assume an influence of the passing of time on the processes underlying decision making [for a review, see 24] need to assume that an internal representation of previous trial durations feed into decision processes, and Moon et al [25] have shown that this approach can be used to inform a fMRI study into the interference between temporal information and encoded length.

This latter study is related to another line of research that focuses on the internal representation of time. According to Walsh's A Theory Of Magnitude [26, 27], any magnitude-related information that is stored in the brain might influence future magnitude processing. Because of this intimate connection between different dimensions, it is essential that a proposed memory system is as flexible as possible, as it might be necessary to explain how space, number, time and any other dimension that can be expressed as a magnitude can influence performance on a future interval timing trial [28].

**Conclusions**

All discussed theories provide support for the claim that a mixture of bottom-up input (the clock-system) and top-down influences (the memory system) determines how an objective duration is subjectively perceived, and reproduced. The Bayesian approaches and the Internal Reference Model provide elegant, mathematical models of how the temporal reference memory system can provide top-down influences on interval timing. On the other hand, when interval timing is an element of more complex tasks, and especially when interval timing is studies in more real-world task environments [29,30], the limited flexibility of these models might prevent successful application, whereas a temporal reference memory system based on a more general memory model can still be applied [see for an example, 31]. As papers focusing on trial-by-trial effects become more common in the field of interval timing [e.g., 32,33,34], incorporating more detailed memory models will become unavoidable.

However, instead of focusing on a single type of model, it is important to realize that all these models share many features with the traditional and highly-successful triad-based interval timing models [16,35]. It is therefore likely that researchers who manage to combine the different types of models will drive future developments, and provide new theories to explain how perceived duration is affected by prior experience [36].

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