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Accounting for memory mechanisms in 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.

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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. 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. A notable exception to the agnostic view of the decision component are some recently proposed theories 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 (parts of) the triad assumed by clock theories [4,5]. With respect to the memory component, most literature simply assumes that a memory system holds a fairly stable and accurate representation of relevant durations that the functioning of this memory system does not directly interfere with temporal performance. 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 toward 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••,9,10]. This regression toward the mean is observed even when the different durations easily distinguishable, for example when they are represented by unique, easily identifiable stimuli [11,12].

Although Vierordt work, published in 1868, demonstrates that 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 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 toward the mean can be observed that is larger for the longer durations than for the shorter durations.

The proposed Bayesian model accounts for this Vierordt-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 toward 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 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 *et al.* [15] specifically focused on the prior, and assessed whether the prior would indeed reflect the properties of the environment. In their experiments, participants were 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 alternative approach [17]).

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