

Bayesian optimization of time perception

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Precise timing is crucial to decision-making and behavioral control, yet subjective time can be easily distorted by various temporal contexts. Application of a Bayesian framework to various forms of contextual calibration reveals that, contrary to popular belief, contextual biases in timing help to optimize overall performance under noisy conditions. Here, we review recent progress in understanding these forms of temporal calibration, and integrate a Bayesian framework with information-processing models of timing. We show that the essential components of a Bayesian framework are closely related to the clock, memory, and decision stages used by these models, and that such an integrated framework offers a new perspective on distortions in timing and time perception that are otherwise difficult to explain.

Introduction

Humans are often surprisingly accurate at timing intervals in the sub-second to minutes range during daily routines, as well as part of vocational and recreational activities [1]. We must judge the correct time to strike the right musical chord, adjust our running speed to be in the right place at the right time to catch a fly ball, and anticipate when to begin pressing the button to open the door when the subway train comes to a stop. However, our subjective experience of time can be highly biased in different contexts [2–8]. For example, sounds are often judged longer than lights, even when they are both of the same physical duration and have been matched for intensity [8]. Traditional timing models suggest that these contextual effects are associated with the differential decay of modality-specific representations, changes in the speed of the ‘internal clock’, and/or ‘memory mixing’ of different temporal representations [5,8–10]. Recently, researchers have used Bayesian inference to perform computational-level analysis on various forms of contextual calibration of interval timing and revealed that such adaptation may help to improve overall performance [6,11–14]. Although

the Bayesian approach to optimization has provided many important insights, exactly how these probabilistic distributions and inferences might be linked to temporal processing at a mechanistic level remains uncertain.

In this article, we review recent progress in understanding the influence of contextual calibration on interval timing, with particular focus on ‘central-tendency’ and ‘modality’ effects, as well as the time-order error (TOE). We then compare the different explanations for contextual calibration made by Bayesian inference and traditional information-processing models of interval timing. Finally, we provide a roadmap for integrating a Bayesian framework with existing timing models and point out the implications and potential challenges associated with this approach.

Contextual calibration of time perception

As noted above, subjective durations can easily be distorted by various contextual factors. A classic example of contextual calibration is Vierordt’s law [15], also known as the ‘central-tendency’ effect. When participants are presented with a range of stimulus durations and are then asked to reproduce those durations, they tend to overproduce ‘short’ durations and underproduce ‘long’ durations. This ‘central-tendency’ effect has been demonstrated in numerous studies (for reviews, see [10,15]). A common explanation of this effect is that duration judgments are derived not only from current sensory inputs, but are also influenced by the acquired statistics (e.g., mean and standard deviation) of the distribution of previously experienced stimulus durations [5,6,8–10,15].

Interestingly, the ‘central-tendency’ effect has been observed to vary across different groups of individuals with various levels of experience, including musical expertise. For example, although individuals with little or no musical training exhibit the ‘central-tendency’ effect for both auditory and visual stimuli, string musicians show very low biases for auditory duration reproduction. Moreover, expert drummers are able to reproduce both auditory and visual durations near perfection [16]. In contrast to healthy individuals, patients with Parkinson’s disease (PD) are more prone to contextual manipulation when tested off of their dopaminergic medication, referred to as a temporal ‘migration’ effect [17]. When PD patients given dopamine-replacement therapy (e.g., L-dopa + apomorphine) are trained to time-specific stimulus durations (e.g., 8 s and

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21 s visual stimuli) using corrective feedback, they are able to reproduce these stimulus durations with the same accuracy and precision as age-matched controls. However, when these same PD patients are tested off of their medication, a strong ‘central-tendency’ effect emerges, even if corrective feedback is given. Under these conditions, the 8 s duration is overproduced and the 21 s duration is underproduced when both durations are presented within the same session, but not when they are presented in separate sessions (Figure 1A).

A second example of contextual dependence is associated with the presentation order of two or more durations, referred to as the time-order error (TOE) [4,18,19]. In this case, the order of presentation can bias the threshold for determining whether a stimulus is shorter or longer than the preceding duration [19] and change the sensitivity of the duration judgment [18,20,21]. The biases in the threshold can be positive or negative depending on various experimental factors, such as the relative lengths of the durations being compared and the inter-stimulus intervals [19,22]. A meta-analysis [18] has revealed that the sensitivity of duration judgments is often worse when the comparison duration is presented prior to the standard duration, compared to the reverse order. The usual explanation for the TOE is similar to accounts proposed for the ‘central-tendency’ effect, namely, participants adapt to the average stimulus duration used within an experimental setting, thereby causing the perceived duration of the first stimulus to ‘gravitate’ toward this remote standard [23]. It is important to note, however, that ‘gravitation to the mean’ does not require a large number of trials, that is, an immediately preceding or succeeding distractor interval is sufficient for participants to ‘assimilate’ compared stimulus durations [13,24].

Another form of contextual calibration is the classic finding that ‘sounds are judged longer than lights’ [25]. When auditory and visual stimuli are intermixed within a session, participants frequently overestimate auditory stimuli and underestimate visual stimuli of equivalent physical durations [8,25–32]. This ‘modality’ effect also occurs for simultaneously presented multimodal durations [12,14,33–35]. For instance, when different auditory and visual stimuli are presented together in an audiovisual temporal bisection task, the perceived audiovisual duration appears to be an integrated estimate of two durations with dominance by the auditory stimulus [14].

Traditional approaches to contextual calibration

A well-known quantitative model that addresses contextual influences on perception is the adaptation-level (AL) theory proposed by Helson [36]. According to this theory, a percept of a stimulus depends on the background context. For example, the perceived luminance of an object is subject to the surrounding luminance. Helson quantitatively describes the background context as the pooled effect of all stimuli (i.e., adaptation level). A modified version of AL theory has been used to explain biases and sensitivity changes induced by the temporal order of presentation [18,19]. In a simplified example,

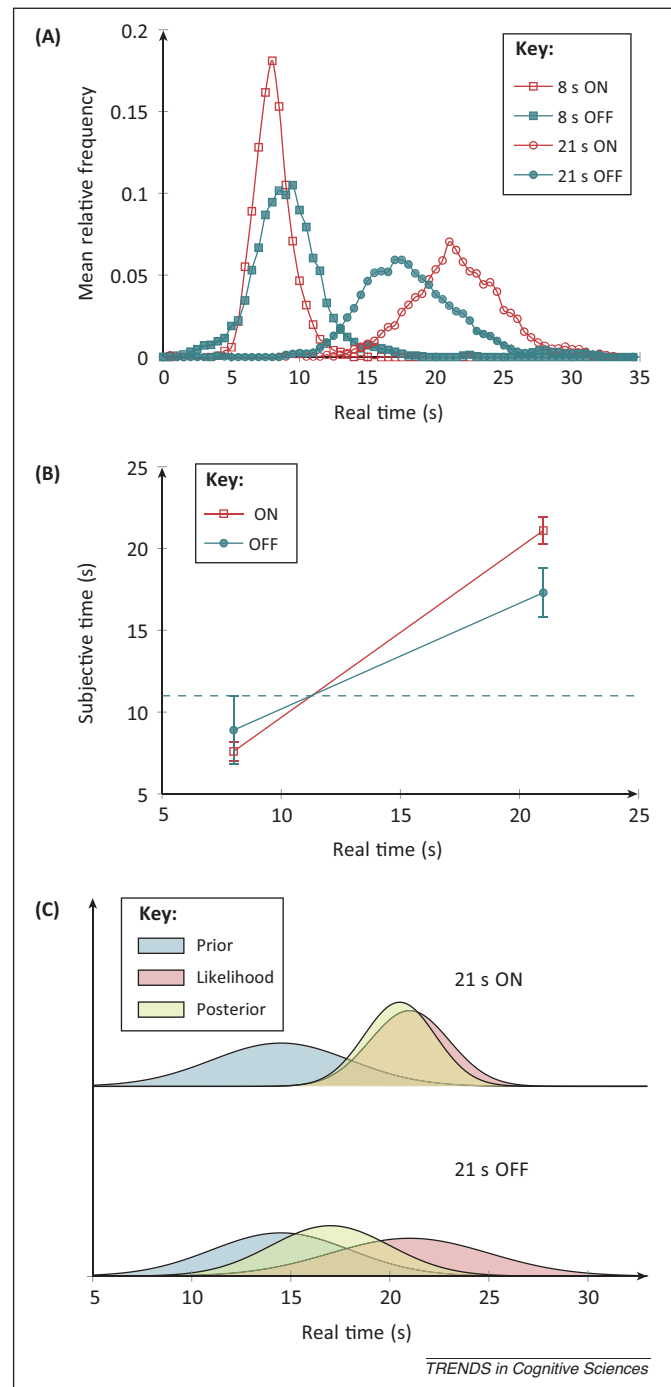


Figure 1. Illustration of the ‘migration’ effect in temporal reproductions of Parkinson’s disease (PD) patients. **(A)** Relative frequency distributions for the two target durations (8 and 21 s) plotted as a function of the medication states. The peak functions illustrate accuracy and precision of duration reproduction in PD patients ON and OFF their dopaminergic medication. In the ON medication state, their accuracy and precision are comparable to age-matched controls. However, in the OFF medication state, a strong central ‘migration’ effect emerges as indicated by shifts of the peak functions. Adapted, with permission, from [17]. **(B)** The subjective peak time plotted against the real time as a function of the medication states. In the OFF medication state, the peak times are biased towards the subjective center of the distribution of duration signals. The dashed line indicates the estimate of the subjective center based on the simple linear-weighted average model (Equation 1). **(C)** Schematic illustration of how Bayesian inference might be applied for the ON and OFF states in 21 s duration reproduction. The withdrawal of the dopaminergic medication in the OFF state may increase uncertainty in the sensory likelihood. Thus, the unchanged prior gains more weight in the final estimate, and the posterior shifts towards the prior.

the perceived subjective interval \hat{d} is a linear weighted average of the sensory evidence and context:

$$\hat{d} = (1 - w)s + wd_p, \quad [1]$$

where s is the rescaled (e.g., logarithmic) value of the stimulus duration, d_p is the subjective expectancy of stimulus durations, and w is the empirically determined weighting constant that can be either positive or negative. When the weight w of the internal expectancy d_p is positive, the perceived duration \hat{d} is attracted toward the center of the distribution. Thus, the simple ‘weighted average’ model also predicts Vierordt’s law for duration discrimination. Figure 1B shows how this linear-weighted model could explain the ‘migration’ effect for the reproduction of stimulus durations observed in PD patients when tested off of their dopaminergic medication.

Scalar timing theory with its clock, memory, and decision stages is the most common heuristic used to describe the cognitive processes involved in the contextual calibration of duration discrimination [5,8–10,37–40]. The hallmark of this model is that the standard deviation of temporal estimates increases linearly with the mean of the duration being estimated – which is referred to as the scalar property (Box 1). Scalar timing theory typically assumes that a memory translation process induces the

scalar property [38,39,41], allowing violations of the scalar property to serve as an indicator of contextual influences on timing and temporal memory. This leads to the ‘memory-mixing’ account of modality differences [8–10], which suggests that contextual calibration arises from the mixing of auditory and visual durations within a shared memory distribution. This account assumes that auditory stimuli drive the clock stage (composed of a pacemaker, switch, and accumulator) at a faster rate than visual stimuli and, as a consequence, the clock readings transferred into memory are proportionally longer for auditory stimuli than for visual stimuli. Consequently, when the current clock reading is compared to a memory sample retrieved from this ‘mixed’ distribution, clock readings for auditory stimuli will be judged (on average) to be longer and visual stimuli (on average) will be judged to be shorter than the mean of the ‘mixed’ distribution. If auditory clock readings are compared only with auditory memories and visual clock readings are compared only with visual memories, no modality differences consistent with changes in clock speed should be observed [8]. An example of the ‘modality’ effect in temporal bisection is illustrated in Figure 2A, where the ‘short’ (S) and ‘long’ (L) anchor durations consist of both auditory and visual stimuli, and intermediate comparison durations of both modalities are randomly

Box 1. Information-processing (IP) models of interval timing and the scalar property

One of the best-developed models of interval timing is scalar timing theory, which belongs to a class of information-processing models that posit a dedicated ‘internal clock’ [5,37–40,77]. According to scalar timing theory, the cognitive processes supporting interval timing consist of three stages: clock, memory, and decision (Figure 1, Box 2). In order to represent a target duration, a pacemaker emits pulses that are passed by a switch into an accumulator. The value in the accumulator is assumed to be normally distributed [60], which is then compared to the expected time sampled from reference memory. If these values are close enough at the decision stage, a response is made. When the entire response function obtained from peak-interval/temporal generalization procedures is plotted on a relative time scale for multiple target durations, the different response functions typically superimpose with each other, which demonstrates that interval timing adheres strongly to Weber’s law [38,41,85–88]. This is called the scalar property of interval timing. Evidence for superimposition in the peak-interval procedure is illustrated in Figure 1 for human participants. Scalar timing theory assumes the scalar property is introduced by a memory translation constant k^* [60,61,64–66], because variances in the clock and decision stages are considered insufficient to account for the scalar property ([38,39,41], but see [54,77]). The memory translation constant k^* is drawn from a normal distribution $N(\mu_{k^*}, \sigma_{k^*})$, such that this multiplication results in wider memory distributions for longer durations than for shorter target durations (Figure 1). Systematic violations of the scalar property can occur when timed intervals are selected from particular ranges or tested with selected clinical populations (e.g., PD patients) [78,86,89,90]. These violations of the scalar property suggest that multiple timing systems may subservise different time scales and that contextual influences should be considered more carefully in theoretical models of timing and time perception.

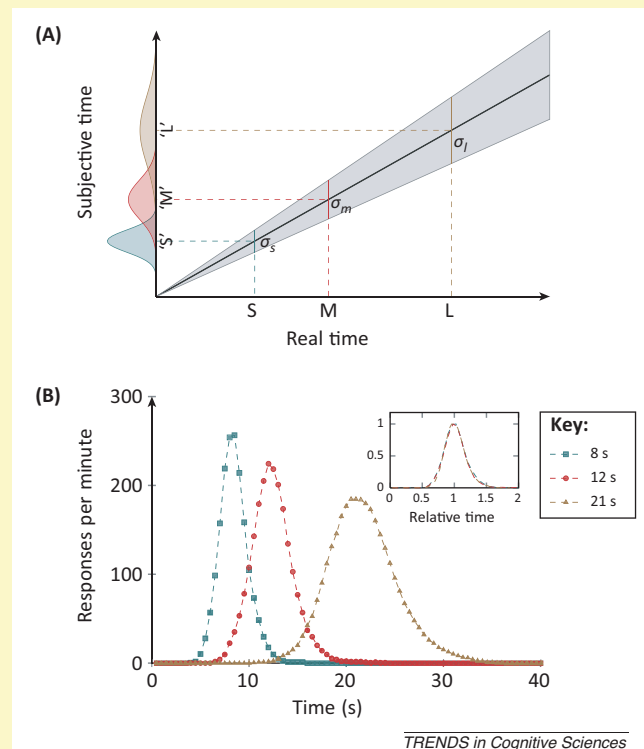


Figure 1. The scalar property of interval timing and evidence of superimposition of peak-interval functions. (A) Scalar timing theory assumes that the estimation error increases in proportion to the target interval (gray area), which leads to the scalar property being exhibited for ‘short’ (S), ‘medium’ (M), and ‘long’ (L) target durations. (B) Evidence of the scalar property from human participants. Mean key presses per minute are plotted as a function of signal duration (s) for participants trained with 8, 12, and 21 s target durations. The inset figure shows that the response functions superimpose on each other when they are plotted as a function of relative time. Adapted, with permission, from [91].

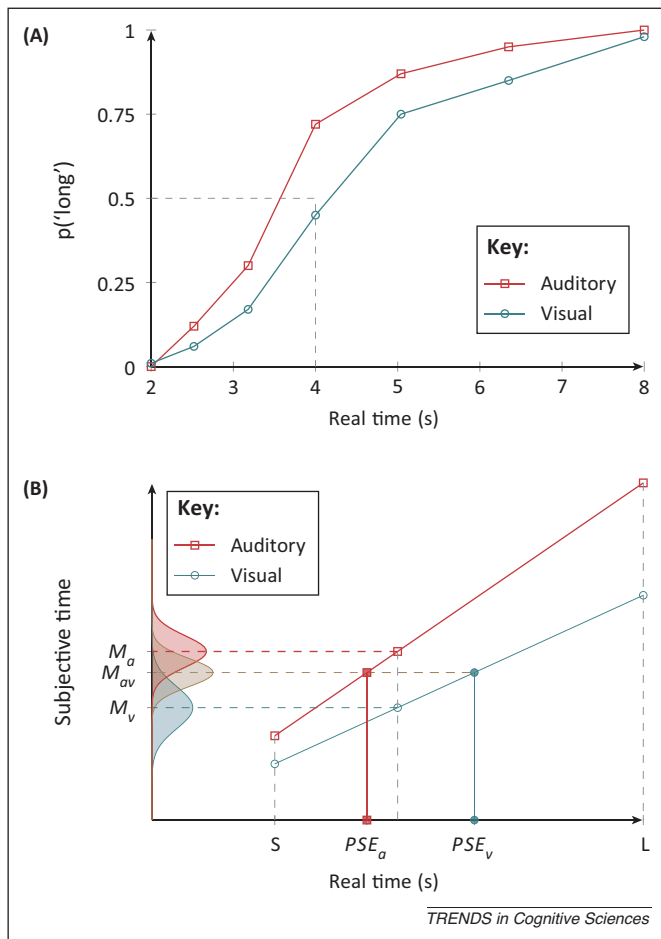


Figure 2. Illustration of the ‘modality’ effect in temporal bisection. **(A)** Group probability of a ‘long’ response, $p('long')$ functions averaged across participants for auditory and visual stimulus durations presented in a 2 s vs 8 s bisection task. Adapted, with permission, from [42]. **(B)** Schematic illustration for a Bayesian inference account of the ‘modality’ effect in which pulses are integrated at a faster rate for auditory stimuli than for visual stimuli due to differential rates of opening and closing of the switch that allows pulses to flow from the pacemaker to the accumulator [8,9]. As a consequence, the internal reference of the mean duration between the ‘short’ (S) and ‘long’ (L) anchor durations is larger for auditory stimuli (M_a) than for visual stimuli (M_v). These different internal representations correspond to the same external duration indicated by the middle vertical dashed line. When the auditory and visual durations are combined or mixed within the same memory distribution, assuming that M_a and M_v are independent Gaussians, the internal reference of the mixed durations (M_{av}) is a linear-weighted average of M_a and M_v . Based on this mixed reference, the auditory and visual points of subjective equality (PSE) are shifted in opposite directions – as indicated by the filled squares and circles, respectively.

intermixed within a session [42]. As a result of this intermixing of stimulus modalities, the point of subjective equality (PSE) observed for auditory durations occurs at an earlier time than the PSE observed for visual durations.

Given that the external world is in constant flux, the mixing of temporal memories is likely to accrue over time in order for the observer to adapt his/her timing behavior. Taatgen and Van Rijn [5], for example, found that the ‘central-tendency’ effect was not only influenced by the mixing of multiple durations, but also fluctuated as a function of feedback and estimates of the stimulus durations experienced on previous trials (recency effect). Similarly, Dyjas *et al.* [18] suggested that TOEs associated with sensitivity changes in duration comparisons are the result

of dynamic updating of internal referents,

$$I_n = gI_{n-1} + (1 - g)X_{1n}, \quad [2]$$

where I is the dynamic history of the internal reference for the first interval and X_{1n} is the current first interval. When the sensory estimate of the current first interval X_{1n} is presented, the mean interval reference I_n is then updated. In these approaches, the weights of prior history and feedback are estimated by fitting a general linear model, which does not indicate whether the system uses an optimal strategy for dynamic updating. Nevertheless, when Equation 2 combines with Bayesian inference, it is referred to as the application of a Kalman filter [43–45]. The g in Equation 2 is referred to as ‘Kalman gain’, which is optimally determined and updated dynamically by the variances of the internal reference and the sensory estimate. The application of a Kalman filter has been supported by a number of empirical studies that examined the ‘central-tendency’ effect of distance reproduction [43,46], sensorimotor control [45], and multimodal recalibration [44,47].

Bayesian inference on temporal contextual calibration

The combination of a linear-weighted average model and scalar timing theory provides a powerful approach to explain various ‘memory-mixing’ phenomena [5,8–10,18], yet these approaches do not inform us as to what factor(s) quantitatively determine the level of contextual calibration. Recent work using a Bayesian approach solves this problem by providing a quantitative prediction of the contribution of temporal context and the mechanisms that involve the subjective representation of duration [6,16,48–51] (Box 2). The basic logic of the Bayesian approach is that sensory measurements are noisy and uncertain, and combining the prior knowledge of the statistical distribution of a series of stimulus durations can be beneficial for increasing the precision of duration estimates, although incorporating the prior may lead to systematic biases. In this sense, contextual effects are statistically optimal and serve to minimize error. Moreover, the trade-off between precision and bias will depend on the magnitude of uncertainty and the selected cost function [48].

An impressive demonstration of how Bayesian inference can be used to predict the ‘central-tendency’ effect in temporal reproduction has been given by Jazayeri and Shadlen [6]. In their study, participants were instructed to estimate a sample duration and reproduce it immediately afterwards. For different blocks of trials, however, the sample durations were selected from three different uniform distributions (i.e., ‘short’, ‘intermediate’, and ‘long’ ranges) that partially overlapped with each other. The results revealed a strong ‘central-tendency’ effect in duration reproduction as illustrated in Figure 3. Jazayeri and Shadlen then used a Bayesian framework to show how different types of observer models with variation in the application of the prior and the estimation error might be used in duration reproduction. They reported that the best-fitted model was the one using a Bayes least-square (BLS) rule (i.e., a square-error loss function; Box 2). The success of the BLS rule suggests that participants used the statistical information provided by the distribution of stimulus

Box 2. Bayesian inference of timing and linkage to information-processing models

Analogous to the classic information-processing (IP) models that involve clock, memory, and decision stages, Bayesian inference has three essential components: likelihood, prior distribution, and loss function [45,48,92,93]. As illustrated in Figure 1, two frameworks are closely linked to each other.

Suppose that we have an external duration D , with an associated internal clock reading S that represents the number of pulses in the accumulator at the end of D . The likelihood function $P(S|D)$ is the probability distribution of obtaining a clock-reading S for a given external duration D . The spread of the likelihood indicates the uncertainty of sensory measurement. At the memory stage, sensory estimates of the target duration update the prior distribution $P(D)$ in reference memory. Meanwhile, the prior knowledge may influence the memory representation of the current clock reading. According to Bayes' rule, the probability of having an external duration D for a given clock-reading S is determined by the sensory likelihood and the prior knowledge of target durations $P(D)$:

$$P(D|S) = \frac{P(S|D)P(D)}{P(S)} \quad \text{[I]}$$

The probability distribution $P(D|S)$ is known as the posterior probability. Given the posterior probability, the Bayesian ideal-observer next has to make an optimal decision or choose an action based on the loss function, a function that specifies how the system rates the relative success or cost of a particular response [45,50,67], that is, the costs associated with a function of

estimation error $(\hat{D} - D)$. The most frequently used loss functions for modeling behavior are the squared-error $L = (\hat{D} - D)^2$ [50,67], or relative squared-error $L' = (1 - D/\hat{D})^2$ functions [50,94]. The latter is comparable to the ratio rule used in classic IP models to achieve the scalar property [38,95].

When the likelihood and the prior are independent Gaussians, that is, $P(S|D) \sim N(\mu_s, \sigma_s)$, $P(D) \sim N(\mu_p, \sigma_p)$, the optimal estimate by minimizing the loss function L is:

$$\hat{d} = (1 - w_p)\mu_s + w_p\mu_p \quad \text{[II]}$$

where $w_p = \frac{1/\sigma_p^2}{1/\sigma_p^2 + 1/\sigma_s^2}$ is proportional to its inversed variances (Figure 1). The variance of this optimal estimate is $\frac{\sigma_p^2\sigma_s^2}{\sigma_p^2 + \sigma_s^2}$, which is the minimum variance among all possible linear weighted combinations between the sensory estimate and the prior [92,93,96]. When there are two conditional independent likelihood functions, and the prior is not the focus factor and can be assumed to be uniform, Bayesian optimization is equivalent to maximum likelihood estimation (MEL). The optimal estimate is also a linear weighted average of individual sensory estimates:

$$\hat{d} = w_a\mu_a + w_b\mu_b \quad \text{[III]}$$

where μ_a and μ_b are the mean estimates of two individual signal durations, and w_a and w_b are their corresponding weights that are proportional to their inversed variances.

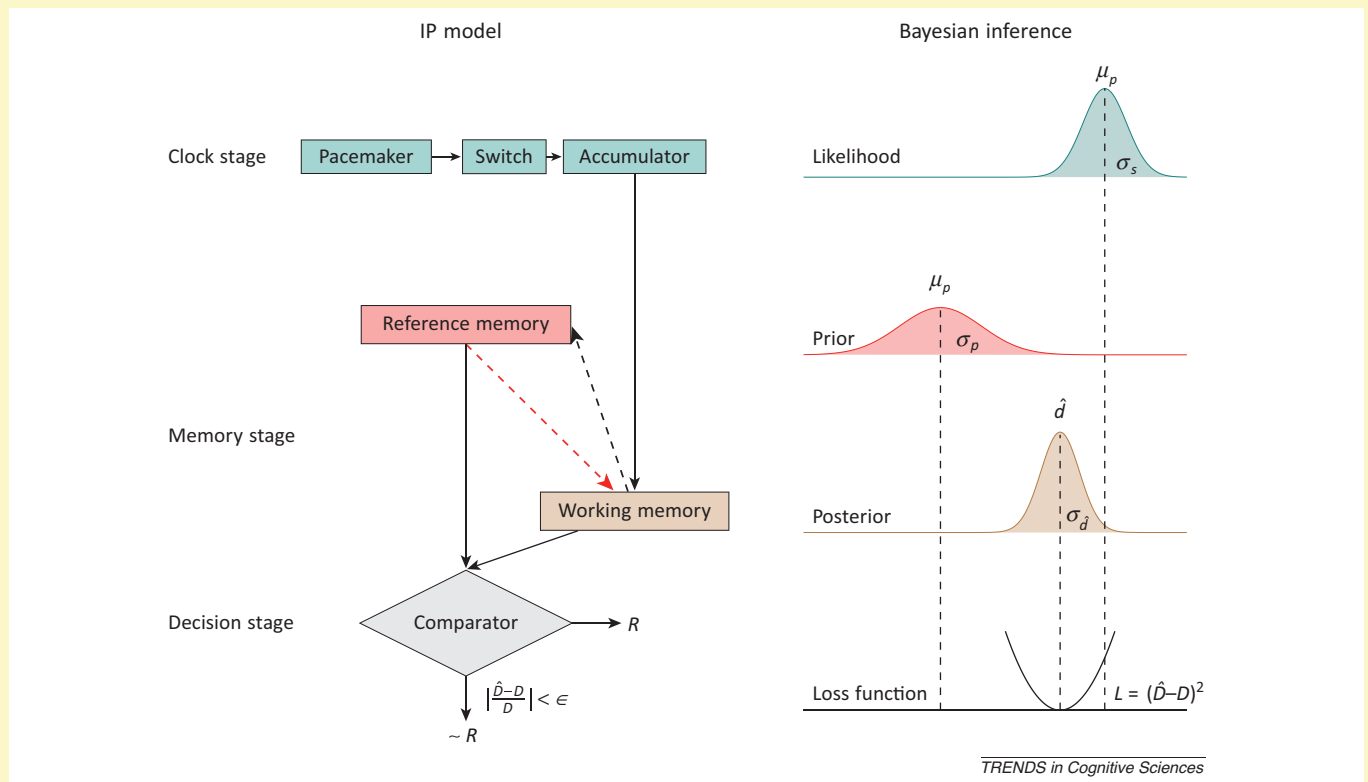


Figure 1. An information-processing (IP) model of scalar timing theory and Bayesian inference of time estimation. The left panel shows an IP model of time perception involving clock, memory, and decision stages. The right panel illustrates that the three key components of Bayesian inference are closely matched to the three stages of the IP model. The sensory likelihood is derived from the clock stage. The prior represents the durations stored in the reference memory, which is updated by current estimates (dashed black arrow). The posterior reflects the probability distribution of the current estimate, combining the clock reading and the influence of the reference memory (indicated by the dashed red arrow). In the decision stage, responses are made based on specific comparison rules. The goal of Bayesian inference is to minimize the loss function, whereas the comparator of the IP model uses a relative discrimination threshold.

durations presented within a block of trials to minimize their overall temporal reproduction error [6].

The 'modality' effect [8] induced by the 'memory mixing' of auditory and visual signals can also be quantitatively modeled using Bayesian inference. Although the exact

decision-rules used in temporal bisection are still under debate [52], one proposal is that a comparison is made between the current trial's clock reading and an internal reference (M) of the mean duration (e.g., geometric mean of S and L). Given that auditory stimuli drive the clock faster

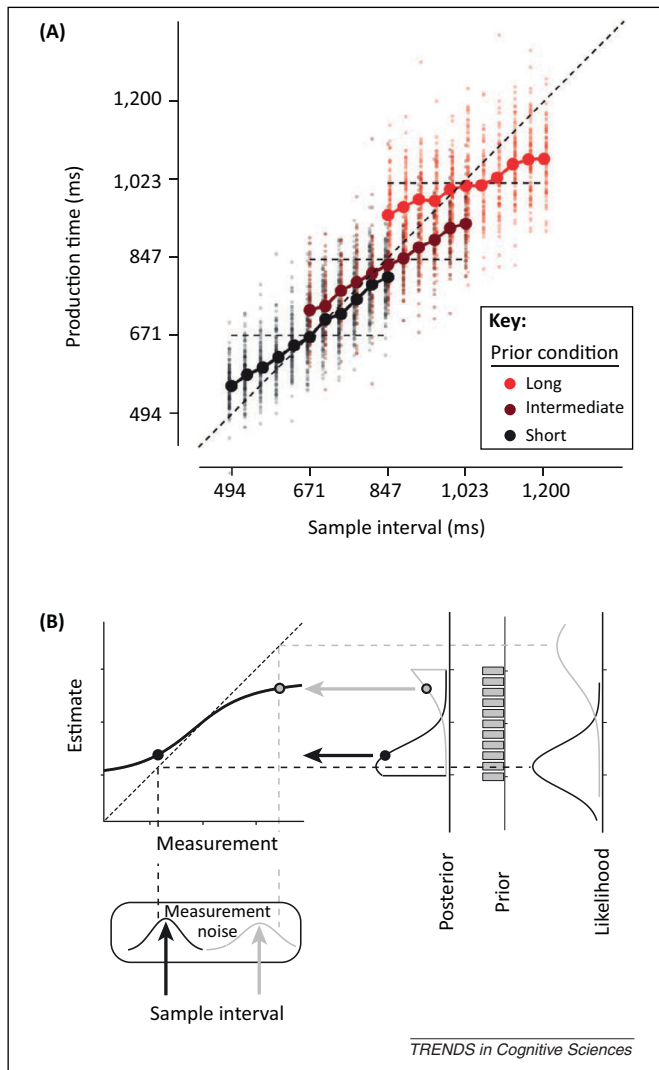


Figure 3. Illustration of the 'central-tendency' effect in temporal reproduction. **(A)** Individual production times for individual trials (small dots) and their averages for each sample interval (large circles connected with thick lines) are shown for three prior conditions for a typical participant. Average production times deviated from the line of equality (diagonal dashed line) toward the mean of the priors (horizontal dashed lines). Prior-dependent biases were strongest for the 'long' prior condition. **(B)** Schematic representations of how Bayesian inference is computed. Upward arrows in black and gray show two example intervals. Vertical dashed lines represent the noise-perturbed measurements associated with those sample intervals. The likelihood function, the prior (distribution of experimental intervals), and the posterior are shown on the far right. The thick dots on the posterior and horizontal arrows show the optimal estimates based on a selected cost function (here, square-error function). Among various observer models, a Bayesian observer associated with the Bayes least-square (BLS) was the best fit. Adapted, with permission, from [6].

than visual stimuli, the internal reference for auditory durations (M_a) will be larger than the internal reference for visual durations (M_v). However, when participants use the same decision criterion and bias, the internal difference between M_a and M_v cannot be observed if the temporal bisection task is conducted separately within auditory or visual modalities. This is because both internal references will be correspondent to the same external (auditory or visual) duration (Figure 2B). However, when auditory and visual durations are randomly mixed, according to Bayesian inference, the internal reference (M_{av}) of the mixed durations will be a linear-weighted average of M_a and M_v with weights proportional to their correspondent

reliability (assuming M_a and M_v are independent Gaussians). When temporal judgments are made based on this mixed internal reference M_{av} , the auditory PSE is shifted earlier, whereas the visual PSE is shifted later in time. As a result, 'sounds are judged longer than lights' and the response pattern corresponding to the classic 'modality' effect emerges as shown in Figure 2A.

Other applications of Bayesian inference to interval timing have shown how the assimilation of an 'entrainment' context can be explained by a linear weighted model (Equation 1) in which the weights are directly proportional to the measured Weber fractions [13]. That is, the uncertainties of the stimulus duration and the background context determine their contributions in the final estimate (Box 2). Similar Bayesian approaches have been applied to multimodal/sensorimotor interval integration [12,14,33,34]. For example, Shi and colleagues [12] tested whether perceptual and motor timing are integrated in an auditory reproduction task by comparing pure motor reproduction, auditory duration comparison, and auditory reproduction. They found that participants incorporate both perceptual and motor timing in an optimal manner in the auditory reproduction task. It should be noted, however, that variances in some conditions, particularly those for short-interval auditory reproduction, are not as small as the model-predicted variances, and do not exhibit the expected improvement. Interestingly, such suboptimal outcomes have been confirmed in several other studies [12,14,33–35], showing that the observed behavioral variability is often larger than predicted by the model [34,35]. A possible reason for this suboptimal integration may be that some of the modeling assumptions, such as independent sensory estimates and Gaussian noise, are not completely fulfilled [53]. For example, time estimates from different sensory modalities may not be statistically independent, as suggested by evidence for a common timing mechanism [7,54,55].

Integrating Bayesian inference with scalar timing theory

As reviewed above, scalar timing theory and Bayesian inference tackle contextual calibration at different levels. Scalar timing theory focuses on cognitive structures and information flow, whereas the Bayesian approach emphasizes computational principles. One of the criticisms levied against the Bayesian approach is that the selection of the likelihood, prior, and loss function is too flexible, and sometimes *ad hoc*. Many data sets can be fitted to support the claim of optimal behavior by selecting the 'appropriate' functions [48,56–58]. In order to avoid the pitfalls of 'Bayesian Fundamentalism', Jones and Love [56] have argued that Bayesian models must be integrated with more mechanistic approaches if they are to serve as genuine psychological theories. In light of this, we compare key components of the Bayesian approach with scalar timing theory [59–63] in order to suggest how these two theoretical frameworks might be profitably integrated.

There are three essential elements in a Bayesian framework: the likelihood, the prior probability, and the loss function for optimization. These elements can be straightforwardly mapped onto the primary information-processing stages of scalar timing theory: the clock, memory, and

decision stages (Box 2). The clock stage is responsible for the measurement of the duration of an external event, which is subject to noise perturbation. The Bayesian likelihood function provides a probability description of a given measurement, conditional on a given physical duration. Scalar timing theory assumes two separate memory representations: a working memory that is able to temporarily store the current clock reading and a reference memory that serves as a long-term store or reference of all recorded clock readings relevant to a particular context. From the Bayesian perspective, the prior quantifies the probability distribution of the internal reference and the posterior represents the probability of the memory representation of the current clock reading. In the end, both frameworks implement some type of decision rule in order to generate a response. In this view, scalar timing theory provides a rational basis for selecting the appropriate Bayesian functions, and the Bayesian framework provides probabilistic descriptions of temporal processing.

Underlying the linkage of the two frameworks, however, are several key differences and a number of important constraints. The main difference comes from the implementation of the scalar property. Scalar timing theory assumes that the scalar property is introduced by the memory constant, k^* , applied during encoding [60,61,64–66]. By contrast, the general Bayesian framework does not provide any specific assumptions concerning the scalar property. However, in experimental applications of Bayesian inference [6,50], the scalar property is often incorporated into the likelihood distribution in order to provide consistency with the obtained data. Recent evidence [50] supports this assumption, suggesting that the scalar property may in fact originate from the clock stage. The second main difference between the two frameworks is in regard to memory updating. In order to account for the effects of contextual calibration, the memory stage of scalar timing theory has been extended from the original working and reference memory components [38,39] to include the processes of ‘memory mixing’ [8–10,40], and dynamic memory updating [5,18]. By contrast, Bayesian inference offers a simple and concise approach for updating memory representations, namely Bayes’ rule. However, selection of the appropriate likelihoods and priors must be done in conjunction with a specific application. The third and final difference that we will discuss involves the decision rules applied by the two frameworks. Scalar timing theory strongly favors a ratio-rule approach (i.e., relative error – Figure I, Box 2) [38,41,52] for duration comparisons, largely because it is compatible with the scalar property introduced by the memory translation constant. In the Bayesian framework, the decision rule is used to minimize the overall error based on a loss function, whereas the loss function depends on a specific application. The most common loss function used by the Bayesian approach is the square-error function (Box 2), which has been shown to be in good agreement with empirical findings [50,67].

Obtaining a better understanding of the interactions between the Bayesian framework and scalar timing theory should help us to develop more robust theories of interval timing that are able to handle various types of contextual calibration, while also shedding light on the manner in

which probabilistic representations are implemented in neural circuits [56,58,68]. For instance, the observation that dopaminergic and cholinergic drugs have different effects on the clock and memory stages of interval timing [61,69–71] suggests that novel pharmacological techniques may provide useful tools for studying the neural implementation of probabilistic representations [72] – although the specific details remain to be tested. Interestingly, the ‘migration’ effects observed in PD patients suggest that the likelihood function is flattened by the withdrawal of dopaminergic medication, which is required to maintain more normal functioning of the clock stage in PD patients. Thus, the unchanged prior gains more weight in the final estimate (Figure 1C). In this manner, dopamine-deficient individuals appear to be able to balance performance by reducing temporal uncertainty at the cost of temporal accuracy [11]. Integrating Bayesian inference with scalar timing theory could also be beneficial in explaining other forms of contextual calibration, including the influences of non-temporal factors (e.g., background intensity, speed/sequence structure) [4,73–75].

Concluding remarks

Under ordinary circumstances, the representations of event durations are ‘calibrated’ by various forms of temporal context. These contextual calibrations include ‘migration’ toward the central tendency of a distribution (Vierordt’s law), TOEs, and modality differences. Application of scalar timing theory suggests that contextual calibration of event durations occurs mainly at the memory stage [8–10]. On the other hand, recent Bayesian approaches point out that the likely reason for such calibration is an effort to improve timed performance by reducing the overall error [6,13,76]. In an effort to resolve these apparent incompatibilities, we have shown that the three essential components of a Bayesian framework (i.e., likelihood, prior, and loss function) are closely linked to the clock, memory, and decision stages advocated by scalar timing theory and incorporated into other timing models [40,69,77]. The matched counterparts of a Bayesian framework combined with scalar timing theory not only provides a forward-looking perspective on interval timing, but also offers quantitative predictions of distortions in temporal memory for normal participants, as well as for individuals with neurological impairments [78,79]. It is worth noting, however, that many aspects of interval timing remain unsolved (Box 3), even for relatively simple temporal

Box 3. Questions for future research

- How can the probabilistic representations of the Bayesian likelihood and prior be implemented in temporal memory?
- Bayesian inference does not explicitly state the source of the scalar property. Do the sensory likelihood, prior, and loss function all exhibit the scalar property?
- Can Bayesian inference readily account for non-temporal forms of contextual calibration (e.g., stimulus intensity effects)?
- What are the ways in which genetic and/or pharmacological profiles can be used to unravel the probabilistic representations and computations used in time perception?
- How can we further integrate the Bayesian framework with other theories, such as the striatal beat-frequency model of interval timing [54,77]?

discrimination and generalization tasks [40,80]. Continued application of an integrated Bayesian framework with mechanistic-level theories, such as scalar timing theory and the striatal beat-frequency model of interval timing [54], should help us to expand our understanding of the functional and neural mechanisms of interval timing [81–84].

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